



**This electronic thesis or dissertation has been  
downloaded from Explore Bristol Research,  
<http://research-information.bristol.ac.uk>**

*Author:*

**Chapman, Will G**

*Title:*

**Embodied Decisions**

*Linking Perceptual Uncertainty and Reach-to-Grasp Trajectories*

**General rights**

Access to the thesis is subject to the Creative Commons Attribution - NonCommercial-No Derivatives 4.0 International Public License. A copy of this may be found at <https://creativecommons.org/licenses/by-nc-nd/4.0/legalcode>. This license sets out your rights and the restrictions that apply to your access to the thesis so it is important you read this before proceeding.

**Take down policy**

Some pages of this thesis may have been removed for copyright restrictions prior to having it been deposited in Explore Bristol Research. However, if you have discovered material within the thesis that you consider to be unlawful e.g. breaches of copyright (either yours or that of a third party) or any other law, including but not limited to those relating to patent, trademark, confidentiality, data protection, obscenity, defamation, libel, then please contact [collections-metadata@bristol.ac.uk](mailto:collections-metadata@bristol.ac.uk) and include the following information in your message:

- Your contact details
- Bibliographic details for the item, including a URL
- An outline nature of the complaint

Your claim will be investigated and, where appropriate, the item in question will be removed from public view as soon as possible.

# Embodied Decisions: Linking Perceptual Uncertainty and Reach-to-Grasp Trajectories

William Chapman

School of Psychological Science

January 2022

A dissertation submitted to the University of Bristol in accordance with the requirements for  
award of the degree of Doctor of Philosophy in the Faculty of Life Sciences

Word Count: 46,982

## Abstract

Traditional approaches to the psychology of judgement and decision-making have made a great deal of progress in understanding the relationship between perception and action by constructing formal theories and instantiating them in computational models. The embodied cognition approach claims that studying only the reaction time and accuracy of decisions risks obscuring the dynamic nature of mental events. A confluence of these approaches has resulted in the rise of mouse tracking to investigate the dynamics of decision-making across many diverse sub-fields within psychology. However, models which link the process of decision-making to the recorded trajectories in mouse tracking experiments are rare, but frequently relied upon to lend mouse tracking research conceptual and theoretical support. Furthermore, there are more “embodied” ways to interact with the world, than pointing and clicking a mouse, such as reaching to grasp.

This thesis aims to investigate whether the uncertainty introduced by perceptual decision-making influences the very ecological action of reaching to grasp an object, and whether this link can be modelled in a similar way to mouse trajectories. During my PhD I developed a novel experimental paradigm to use three-dimensional motion tracking to record reach-to-grasp movements in an experiment which balanced the rigor of traditional decision-making experiments with more everyday actions. These data were analysed using sophisticated statistical techniques including linear mixed modelling and distribution parameter fitting. An existing computational model which links noisy perceptual evidence accumulation to mouse path generation using embodied cognition principles was developed further to account for the additional complexity of three-dimensional reaches to grasp.

Overall, I found evidence that the reach-to-grasp actions took longer and were more curved when enacted with increased perceptual uncertainty. I concluded that these effects could not be entirely isolated to trials where there was a clear change of mind, but to a wider subset of reaches which were generated by a process distinct from the baseline trials. In addition, the computational model did not satisfactorily recreate the distributions of choice reach curvature generated by participants but indicated that there is a more complex relationship between decision dynamics and reach actions than is typically assumed by strong theories of embodied cognition.

## Acknowledgements

I have been very fortunate to be supported by many brilliant and kind people throughout my PhD.

Firstly, I would like to thank my primary supervisor Casimir Ludwig and my secondary supervisor Iain Gilchrist for giving me the opportunity to complete a PhD with them. I can't express properly the depths of my gratitude for the superhuman levels of patience and support I received from Casimir as both an academic mentor and friend, during a very, let's say, interesting time.

There is a very long list of amazing, lovely and unique people that I have been lucky enough to become friends at my time here at the School of Psychological Science (so far). Deserving of special mention are Nick Martin, Steph Suddell, Ella Gale, Maren Muller-Glodde, Nancy McBride, and Jane Cowan for being with me through thick and thin and sharing cigarettes. Greig Dickson and Hugo Hammond saw me through the last few months writing, and I expect more discussions about the most efficient ways to avoid work with R coding in the future. A special thanks to Jeremy Burn for his own style of encouragement as well.

Finally, I would like to thank Valentina for being the best thing that has ever happened to me. And my parents for their continuing love and support to never give up on my goals, no matter how long they may take.

## Author's Declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's Regulations and Code of Practice for Research Degree Programmes and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

SIGNED: ..... DATE: .....28.01.2022.....

# Table of Contents

Table of Figures .....	x
Table of Tables .....	xiv
Chapter 1      General Introduction .....	15
1.1      Modelling Decision-Making.....	18
1.1.1      Early models of perceptual decision-making .....	19
1.1.2      Evidence accumulation models.....	21
1.1.3      Interpreting drift diffusion model parameters .....	24
1.1.4      Neural signatures of evidence accumulation.....	26
1.1.5      The loci of decision and action.....	28
1.2      Moving beyond the pushing of buttons to record responses .....	30
1.2.1      Response competition in mouse movements and their measurement .....	31
1.2.2      Using trajectory information to find evidence of dynamic decision-making .....	33
1.2.3      Dynamic decisions as an artefact of trajectory averaging .....	35
1.2.4      Dynamic decisions as an artefact of study design .....	36
1.2.5      How dynamic is it really? .....	38
1.3      The control of reaching movements.....	39
1.3.1      The planning and execution of direct goal-directed movements.....	40
1.3.2      The planning and generation of curved goal-directed movements .....	43
1.3.3      The execution of movements to multiple targets .....	45
1.4      Linking accumulator models to response dynamics .....	49
1.5      Conclusion .....	55

1.6	Thesis Outline .....	56
Chapter 2 Increased perceptual uncertainty during timed reach-to-grasp actions increases path deviation 59		
2.1	Background and rationale.....	60
2.1.1	Reaching to grasp movements .....	62
2.1.2	Online control of reach-to-grasp .....	63
2.1.3	Overarching question .....	64
2.1.4	Specific Hypotheses .....	67
2.2	Methods.....	68
2.2.1	Participants .....	68
2.2.2	Design .....	69
2.2.3	Materials .....	69
2.2.4	Procedure.....	71
2.2.5	Data Processing.....	72
2.2.6	Statistical Analysis.....	76
2.3	Results.....	78
2.3.1	Experiment 1.....	78
2.3.2	Experiment 1: Statistical Analysis .....	86
2.3.3	Experiment 2.....	90
2.3.4	Experiment 2: Statistical Analysis .....	98
2.3.5	Comparison of Experiments 1 and 2.....	100
2.3.6	Workspace effects .....	107

2.3.7	Relationships between curvature and timing variables .....	108
2.3.8	Grasp characteristics .....	111
2.4	Discussion .....	112
2.5	Conclusion .....	116
Chapter 3	The curvature of reach-to-grasp trajectories launched during perceptual choice emerge from separable processes .....	119
3.1	Introduction.....	120
3.2	Method.....	124
3.2.1	Participants.....	124
3.2.2	Design .....	124
3.2.3	Materials .....	124
3.2.4	Procedure .....	125
3.2.5	Data Processing .....	125
3.2.6	Statistical Analysis .....	126
3.3	Results .....	126
3.3.1	Reach path differences .....	127
3.3.2	Average reach timing and curvature measures .....	130
3.3.3	Linear mixed model analyses .....	131
3.3.4	Distributional Analysis.....	140
3.4	Discussion .....	150
3.5	Conclusion .....	154
Chapter 4	Simulating the link between evidence accumulation and reach paths .....	156



4.1	Overview .....	156
4.2	Introduction .....	157
4.3	Linking decision theoretic models and reaching trajectories.....	160
4.3.1	Stage 1: Generate random walks.....	161
4.3.2	Stage 2: Generate trajectories using an action focus .....	162
4.3.3	Stage 3: Feedback the position of the effector into the decision variable as a commitment effect. ....	162
4.3.4	Stage 4: Calculating the AUC curvature metric for each simulated trajectory ....	163
4.4	Parameter Exploration.....	166
4.4.1	Single parameter variations.....	166
4.4.2	Parameter interactions.....	171
4.5	Adapting the model to accommodate variability from biomechanical constraints and workspace effects. ....	173
4.6	Alternative model formulation including variability in starting point.....	179
4.7	Discussion .....	184
4.7.1	Biomechanical and non-decision influences on reach path.....	187
4.8	Conclusion.....	192
Chapter 5	General Discussion.....	193
5.1	Aims of the thesis .....	194
5.2	Summary of main findings .....	195
5.3	Interpretation in context of literature .....	200
5.4	Contribution of the work .....	204

5.5	Limitations.....	205
5.6	Overall Conclusion.....	209
	References.....	210
	Appendix A Additional Figures for Chapter 2.....	236
	Appendix B Additional Figures for Chapter 3.....	253
	Appendix C Additional figures for Chapter 4 .....	263

## Table of Figures

Figure 1-1 Schematic of the Drift Diffusion Model of Decision-Making .....	24
Figure 1-2 An Example of the Typical Set Up of a Mouse Tracking Study and Trajectory Measurements.....	33
Figure 1-3 Schematic of Potential Trajectory Types in either a Dual Process or a Dynamic Process .....	34
Figure 1-4 Example of Trajectory Prototypes from Kieslich et al. (2020).....	36
Figure 1-5 Wrist paths of reaches from Tipper, Howard and Jackson (1997) .....	44
Figure 1-6 Experimental Set Up and Trajectories from Flash and Henis (1995) .....	47
Figure 1-7 Four potential models to link decision-making to mouse path trajectories.....	50
Figure 2-1 Schematic of models and their hallmarks of those effects in reach-to-grasp trajectories.....	66
Figure 2-2 Experiment Set Up and Stimuli.....	70
Figure 2-3 Schematic of A Reach and Retrieve Action .....	74
Figure 2-4 Four Sample Trajectories.....	75
Figure 2-5 Overall time between trial start and grasp for experiment 1 .....	80
Figure 2-6 Reach initiation time for experiment 1. ....	82
Figure 2-7 Movement time for experiment 1.....	83
Figure 2-8 Mean curvature as signed Area Under Curve .....	84
Figure 2-9 Experiment 1 Raw and Mean Trajectories .....	85
Figure 2-10 Mean reach paths in experiment 1, overlaid .....	86
Figure 2-11 Overall time between trial start and grasp for experiment 2. Error bars represent within participant standard error. ....	93
Figure 2-12 Reach initiation time for experiment 2. ....	94
Figure 2-13 Movement time for experiment 2, error bars represent within participant standard error .....	95

Figure 2-14 Mean curvature as signed Area Under Curve, error bars represent within participant standard error. ....	96
Figure 2-15 Experiment 2 Raw and Mean Trajectories.....	97
Figure 2-16 Mean reach paths in experiment 2.....	98
Figure 2-17 Overall reach times in both experiments .....	102
Figure 2-18 Overall reach time for both experiments, without change of mind trials.....	102
Figure 2-19 Initiation time in both experiments .....	103
Figure 2-20 Initiation time in both experiments, without change of mind trials .....	104
Figure 2-21 Movement time for both experiments .....	105
Figure 2-22 Movement time for both experiments, with changes of mind removed.....	105
Figure 2-23 Curvature values for both experiments.....	106
Figure 2-24 Curvature values for both experiments, with changes of mind removed.....	107
Figure 2-25 Experiment 1 initiation time quintile and AUC plot .....	108
Figure 2-26 Experiment 2 initiation time quintile and AUC plot .....	109
Figure 2-27 Movement time and AUC, experiment 1.....	110
Figure 2-28 Movement time and AUC, experiment 2.....	111
Figure 3-1 Participant 4 mean reach trajectories and individual trial paths .....	128
Figure 3-2 Distribution of AUCs for participant 4 .....	129
Figure 3-3 Timing and curvature measurements for all data .....	130
Figure 3-4 Average curvature values for experiment 3 with changes of mind removed .....	135
Figure 3-5 Curvature vs initiation time for all successful reaches in experiment 3.....	137
Figure 3-6 Probability of an initial reach to the right.....	140
Figure 3-7 Baseline AUC distributions, with fitted ex-Gaussian curves.....	142
Figure 3-8 Best fit probability functions for the hard choice condition curvatures for participant four. ....	145

Figure 3-9 Hard choice curvature distributions for each participant, baseline and mixed model fits. ....	149
Figure 4-1 Three realisations of the continuous flow with commitment model. ....	164
Figure 4-2 Simulated AUCs and mean trajectories contingent on drift rate. ....	168
Figure 4-3 Simulated AUCs and mean trajectories contingent on boundary separation value... ..	169
Figure 4-4 Curvature distribution and mean trajectory as commitment gain varied. ....	170
Figure 4-5 Curvature distributions and mean trajectories as drift rate and gain are varied. ....	171
Figure 4-6 Curvature distributions and mean trajectories as boundary and gain parameters are varied. ....	172
Figure 4-7 Curvature distributions and mean trajectories as the decision boundary and drift rate were varied .....	173
Figure 4-8 Hard-choice distribution (participant 4) and a simulated curvature distribution using the continuous flow with commitment model.....	174
Figure 4-9 Illustration of the effect of combining a simulated curvature distribution and a baseline .....	177
Figure 4-10 Four sets of baseline-modified simulated reach curvatures, with an empirical hard-choice distribution as comparison.....	178
Figure 4-11 Unmodified simulated trajectories, with a close-up of the start location .....	179
Figure 4-12 Trajectory simulations with starting points at the decision boundaries.....	181
Figure 4-13 Simulated trajectories and curvature distributions for participant 4 .....	184
Figure A-1 Raw and filtered position and derivative of a single trial from experiment 1 .....	236
Figure A-3 Wrist orientation over time in experiment 1 .....	249
Figure A-4 Study 1 wrist orientation traces, overlaid .....	250
Figure A-5 Study 2 wrist orientation.....	251
Figure A-6 Study 2 wrist orientation overlaid.....	252

Figure B-1 Trial paths and mean path for participant 1 .....	253
Figure B-2 Trial paths and mean path for participant 2 .....	253
Figure B-3 Trial paths and mean path for participant 3 .....	254
Figure B-4 Trial paths and mean path for participant 4 .....	255
Figure B-5 Trial paths and mean path for participant 5 .....	256
Figure B-6 Curvature boxplot for participant 1 .....	257
Figure B-7 Curvature boxplot for participant 2 .....	258
Figure B-8 Curvature boxplot for participant 3 .....	258
Figure B-9 Curvature boxplot for participant 4 .....	259
Figure B-10 Curvature boxplot for participant 5 .....	259
Figure B-2 Median and mean trial paths for experiment 3 .....	260
Figure C-1 Simulated trajectories and curvature distributions as decision boundary varied .....	263
Figure C-2 Simulated trajectories and curvature distributions as commitment gain varied .....	264
Figure C-3 Simulated trajectories, baseline modified AUC distribution and hard choice AUC distribution for participant 1 .....	265
Figure C-4 Simulated trajectories, baseline modified AUC distribution and hard choice AUC distribution for participant 2 .....	265
Figure C-5 Simulated trajectories, baseline modified AUC distribution and hard choice AUC distribution for participant 3 .....	265
Figure C-6 Simulated trajectories, baseline modified AUC distribution and hard choice AUC distribution for participant 4 .....	266
Figure C-7 Simulated trajectories, baseline modified AUC distribution and hard choice AUC distribution for participant 5 .....	266

## Table of Tables

Table 2-1 Count and proportion for each reach type within choice difficulty condition.....	78
Table 2-2 Regression Coefficients and Standard Errors of Fixed Effects for Each Outcome Measure in Experiment 1.....	87
Table 2-3 Regression Coefficients and Standard Errors for Each Outcome Measure in Experiment 1, With Change of Mind Trials Excluded.....	88
Table 2-4 Influential factors on mean AUC, experiment 1 .....	89
Table 2-5 Count and proportion of reaches initiated before 400ms .....	91
Table 2-6 Mean and range of reach initiations before 400ms .....	91
Table 2-7 Count and proportion of trajectory types recorded in Experiment 2 .....	92
Table 2-8 Regression Coefficients and Standard Deviations of Random Effects and Standard Errors of Fixed Effects for Each Outcome Measure in Experiment 2 .....	99
Table 2-9 Regression coefficients and standard deviations of random effects and standard errors of fixed effects for the models with "change of mind" trials removed and after backwards selection.....	100
Table 3-1 Number and percentage of trials of incorrect reach actions for each participant .....	131
Table 3-2 Regression coefficients and standard errors for main effects and interactions for experiment 3 (comparing Easy and Hard difficulty trials) .....	132
Table 3-3 Number and percentage of change of mind trials for each participant in each choice condition .....	133
Table 3-4 Regression coefficients and standard errors for main effects and interactions for experiment 3, with change of mind trials removed .....	134
Table 3-5 The direction of initial reaches, conditioned on initiation time quintile and target side .....	138
Table 3-6 Model comparison of mixed effects logistic regression .....	139
Table 3-7 Descriptions of each model and the free parameters for each distribution model ....	144

Table 3-8 Parameter fits and AICs for each model variation fit to data from participant four ....	147
Table 3-9 Easy choice condition best fitting models.....	148
Table 3-10 Hard choice condition best fitting models .....	148
Table 4-1 Single parameter variations in decision model.....	166
Table A-1 Effects vs Analysis choice – Experiment 1 Initiation Time .....	237
Table A-2 Effects vs Analysis choice – Experiment 1 Movement Time.....	239
Table A-3 Effects vs Analysis choice – Experiment 1 Overall Time .....	241
Table A-4 Effects vs Analysis choice – Experiment 1 Curvature .....	243
Table A-5 Effects vs analysis choice – Experiment 2 Initiation Time .....	245
Table A-6 Effects vs Analysis choice – Experiment 2 Movement Time.....	246
Table A-7 Effects vs Analysis choice – Experiment 2 Overall Time .....	247
Table A-8 Effects vs Analysis choice – Experiment 2 Curvature .....	248
Table B-1 Linear mixed model output comparing all difficulty conditions for experiment 3.....	262

## Chapter 1 General Introduction

This thesis is about the relationship between perceptual decision-making and reaching-to-grasp movements. There is a currently debate in the literature about whether curved reaching trajectories elicited in choice reaching tasks reflect a single motor plan which is selected and then acted upon (and perhaps updated or overwritten to produce curvature), or whether curvature emerges from the interaction and interference between multiple and simultaneously active action goals as the movement itself proceeds (Alhussein & Smith, 2021; Enachescu et al., 2021; Kim et al., 2021).



This debate exists, in part, because there is an ongoing tension between conflicting approaches to scientific psychology. On one side of the debate are the cognitivists who regard the processes of perception, cognition, and action as stages in an information processing pipeline (Hurley, 2001), and is still the mainstream view (Laird et al., 2017). In this view, each processing stage applies algorithms to transform input information into outputs sent to the next stage. The perceptual stage transforms sense data into abstract mental representations, the cognitive stage performs computations on those representations to select an appropriate action, and the motor system then translates that action into the control signals which are sent to muscles. The mind is separated from the world by the body, and it is the work of psychologists to work out the algorithmic rules governing each stage of processing, without necessarily being concerned with how these are implemented (Marr & Poggio, 1976). When it comes to decisions and how they are acted upon, choosing is therefore about deciding which goal is most preferred, and the outcome of that choice is selecting and triggering the action needed to achieve that goal.

An alternative to this traditional account is the “ecological” approach to perception and action, as pioneered by the work of JJ Gibson (1986). Critics regard the cognitivist position as reductionist (Brette, 2022; Cisek, 1999) as well as reifying a materialist version of mind-body dualism, which psychology usually claims to reject (Read, 2008). In contrast, the target of investigation for ecological psychology is how, without needing to propose the rich internal representations usually implied by cognitivism, complex adaptive behaviour can emerge from the dynamical system of the interaction between the organism and the environment (Clark, 1999; Heras-Escribano, 2021). Instead of perception being the indirect, passive experience of sensations which have been transformed, abstracted and re-presented to cognitive algorithms, the environment and objects within it are instead directly perceived for the opportunities for action, or *affordances*, that they offer to the agent (Heft, 1989). Building on this approach, the embodied cognition framework (Schöner, 2008) further suggests that since ecological decisions are based on a competition between actions, the physical constraints on those actions may

themselves feed-back into the decision-making process (Cos et al., 2011, 2021a, 2021b; Lepora & Pezzulo, 2015). The act of choosing, for the ecological or embodied approach, is thus the resolution of competition between the actions themselves, not abstract representations of them (Cisek, 2007).

It is also important to consider how each of the above approaches support different theoretical positions about human motor control, and whether it is primarily a system which utilises internal models, or primarily a dynamic interaction between an organism and its environment (Schaal et al., 2007). Optimal Motor Control (OMC) is the mainstream information-processing account (Diedrichsen et al., 2010; Todorov & Jordan, 2002; Yeo et al., 2016). Under OMC, the motor control system is constructed of controllers and estimators which do their best to transform an abstract movement-goal into the appropriate afferent neural signals. To achieve this, an optimal controller typically needs both an internal model of limb and object dynamics and some way to balance between costly trade-offs, such as between speed and accuracy, or between movement smoothness and energetic expenditure, all while accounting for both external and internal sources of noise (Yeo et al., 2016).

For the ecological theorists such explicit computations are superfluous: by (for example) leveraging the spring-like properties of muscles and tendons and reflex arcs, the only control signal needed for a point-to-point movement would be the difference between the current state of the musculo-skeletal system and the desired final state of that system (Latash et al., 2010). Instead of needing to work out a trajectory before movement initiation from the parameters of an internal model, a sufficiently “optimised” trajectory will emerge as the difference between the current state and the goal state is reduced over time (Arbib & Bonaiuto, 2016).

In summary, the traditional information-processing account of perception, cognition and action, which separates the decision and the movement, would explain curved reaching movements as either the result of a single movement goal being overwritten after a change of mind, or because

a curved path allows more optimal performance in a task. On the other hand, the ecological approach would explain curved reaching movements as the result of on-line dynamic competition between movement goals resolving as the decision itself proceeds.

The remainder of this chapter reviews the theoretical and empirical background which is relevant to this debate. Section 1.1 (Modelling Decision Making) reviews computational models of decision-making, how the parameters of those models are often interpreted, and neural evidence which points to a close link between decision and action. Section 1.2 (Moving Beyond the Button Press) moves the discussion towards methods which have claimed to better capture the “dynamics” of decision-making through tracking mouse paths. Section 1.3 (The Control of Reaching Movements) reviews motor control in more detail and different positions on the origin of curved movement trajectories. Section 1.4 outlines a possible way to link computational models of decision making to movement execution. Finally, the structure of the thesis is outlined, pointing out how the empirical work within it will investigate the influence of decision making on movement, and simulation work which will investigate the influence of movement on decision making.

Overall, the work in this thesis can be placed in the context of investigating the interdependence of decision-making and action within the embodied cognition framework, and exploring how computational models of decision making may be connected with reach-to-grasp actions.

## *1.1 Modelling Decision-Making*

To “decide” means to commit to a certain course of action, often after gathering evidence which has a decent correspondence with the world, and it is a fundamental part of cognition. As human beings we are faced with decisions all the time, both important and trivial. An important decision might be what course to study, and we would gather evidence from friends, colleagues,

and prospectuses before committing to it by signing on a dotted line. A trivial decision might be which flavour of ice cream to eat, and we would gather evidence by interrogating our own preference at the time, committing to that choice when we grasp the tub lid. The simplest decisions, studied widely in cognitive psychology, are perceptual. To judge which line is longer, which bulb is brighter or what direction something is moving in may be seen as a model system of the process of gathering evidence before committing to a response.

#### 1.1.1 Early models of perceptual decision-making

Early introspective, behaviourist and psychophysical investigators into why some perceptual decisions took longer than others suggested their subjects spent this time switching internally between options. Somehow they were stuck for a while, unable to make up their mind about whether the length of a line (Henmon, 1911), the intensity of a light source (Tolman, 1926), or the pitch of an auditory tone was greater or lesser in magnitude than a benchmark (Muenzinger & Gentry, 1931). The behaviourists noticed that sometimes rats would pause and turn to face each possible direction in a T or Y-shaped maze several times before continuing on (Muenzinger, 1938), behaviours referred to as *vicarious* trial and error (VTE). The animals, like the humans, were “lost in thought”, stuck in place while deliberating over their decision; the human beings had just learned to not wiggle their noses quite so much.

Cartwright and Festinger (1943) were the first to link internal noisy processes to the duration of decisions. Moving within the “phenomenal field” from a state of indecision to a state of certainty took time, and one’s velocity and heading through that field in turn depended on the sum of often opposing forces. There are “driving forces”, pushing the person towards one decision or another and a “restraining force”, exerting caution. For example, during a line comparison task where the subject is to say whether a stimulus line is longer or shorter than a comparison line, there will be one driving force associated with the response “longer” and a complimentary “shorter” force, and each force can vary in both strength and direction. If the trial is easy

(e.g., the stimulus is obviously larger than the standard), then the force pushing her towards the “longer” response will be consistently strong and positive, perhaps facilitated by a strongly negative opposition. However, on a more ambiguous trial both the “longer” and “shorter” driving forces may both be on average slightly positive. Momentary random fluctuations in the strength and direction of each force may suddenly sum together and cause a rapid but incorrect decision. To guard against this, the sum of driving forces at any instant must overwhelm the restraining force, with which the speed-accuracy trade off is implemented. Decision times are therefore lengthened by a stronger restraining force, forcing slower, gradual movement towards a careful decision. Cartwright and Festinger could then construct response time and accuracy curves from the interaction of probabilistic internal forces. Fast errors in this model were due to the confluence of momentarily stronger driving forces and a momentarily weaker restraining force.

Instead of an extra restraining force, Audley (1960) suggested instead that the timing of a response may be down to how long it takes to generate a sufficient run of identical VTE-like responses. The internal VTE responses are modelled as a Poisson process to relate the accuracy and latency of responses to the probability of the stimuli. For example, in a choice task with explicit responses A and B, each associated with VTEs  $a$  and  $b$ , the response A, will happen after a continuous sequence of  $a$  VTEs, and the length of this sequence dependent on balance between accuracy and speed for that participant. During any decision there will be a sequence of VTEs, say *abbabaabaaa*, with the sequence of *bb* triggering a fast B response, or the sequence *aaa* a much slower A response. Hence, fast correct decisions will be more likely when the probability of A is very high regardless of sequence length. Fast error responses will occur if the probabilities of A and B are similar and long enough “run” occurs by chance.

Other models to explain fast errors were proposed around the same time. The fast guess model (Ollman, 1966; Yellott, 1971) suggested that participants trade-off speed for accuracy by

downplaying the strategy of waiting to recognise the correct response (through progressively more accurate template matching) or choosing instead to just guess the answer. In a critical step, Stone (1960) took Audley's runs model a step further and suggested that instead of counting the length of a "run" of covert decisions without considering the history before that point, the mechanism underlying the accuracy and timing of perceptual decisions was the accumulation of evidence to a boundary.

#### 1.1.2 Evidence accumulation models

Up until now, most "pre-decision" activity was assumed to be sub-threshold vacillations in momentary judgement before a stronger single judgement, or time spent in a near equilibrium state of indecision before Cartwright and Festinger's (1943) restraining force opened the gate to an explicit response. A parallel development in mathematical theories of perceptual decision making was signal detection theory (SDT), which describes how an "optimal" decision maker might set internal thresholds to control for false alarms and correct rejections when trying to distinguish the presence or absence of a stimulus in a noisy environment (Tanner Jr. & Swets, 1954). Under SDT the signal and the noise are modelled as overlapping gaussian distributions, and the numbers of hits, misses, false alarms and correct rejections can be used to infer the sensitivity and bias of the decision-maker (Stanislaw & Todorov, 1999).

For these early models, the transition from deliberation of all alternatives to the decision to pick one alternative was instantaneous and probabilistic. The accumulator class of models, on the other hand, do not regard judgements as instant, just incomplete, until there is enough evidence to commit to a decision (Evans & Wagenmakers, 2020), with "enough" defined according to rewards and risks of the task at hand (Bogacz et al., 2006). Stone's (1960) random walk model suggested that at each time step during a trial a sample from a noisy, internal representation of the stimulus is drawn and passed to the accumulator and a decision was made when this

accumulated evidence crossed an internal caution threshold. Instead of an instantaneous switch, there is a gradual movement to a state of decision.

The covert or sub-threshold decisions made at each discrete time step in Audley or Stone's models could be conceived as signal detection events so the process of decision making can be modelled as a series of sequential SDT-like processes (Bogacz et al., 2006; Gold & Shadlen, 2007). The Sequential Probability Ratio Test (SPRT), which captures the same features of statistical optimality as SDT (Griffith et al., 2021; Wald & Wolfowitz, 1948), assumes repetitive sampling of noisy evidence in discrete time steps, and each sample adds to the evidence for, or against, a hypothesis about the environment. Overall, evidence accumulation describes a family of computational models of decision-making, all of which implement at least a *decision variable*, which represents the current state of evidence at a time, and a *response threshold* which represents the cautiousness of the responder (Heitz, 2014; Ratcliff et al., 2016).

Utilising equations which describe the Brownian motion, Ratcliff (1978) extended the idea from a random walk in discrete time into a diffusion process over continuous time, in what eventually became known as the Drift Diffusion Model (DDM) of decision-making. The classic DDM accounts for rapid decision making in two-choice situations assuming a single decision variable which accumulates noisily and continuously towards one of two response thresholds. Even though the mean drift rate will push the evidence accumulator to the correct choice most of the time, the noise in the process will both vary the time that the response boundary is reached, and cause occasional decisions to be incorrect. Having one decision variable and two response thresholds means that the decision variable represents the relative evidence for one proposition over another.

Other decision models feature variations on the evidence accumulation to bound process. The Linear Ballistic Accumulator (LBA) is one of these, and instead of counting relative evidence for one option over another, suggests (for a binary choice task) a race between two independent

accumulators, or multiple accumulators for a task with multiple options (Brown & Heathcote, 2008). There are yet more alternatives to modelling the decision process, which don't involve accumulation. The urgency gating model (UGM) incorporates a mechanism to lower the response threshold as time passes, and only really accumulates the most recent evidence, discarding all but the last few milliseconds (Thura et al., 2012). The leaky competing accumulator model (LCA) similarly allows older evidence to be discarded (Usher & McClelland, 2001).

Each of these modelling approaches have been used to explain departures from the predictions of the DDM in empirical data (e.g. LCA, UGM) or to simplify the computational task of fitting empirical data (e.g. LBA). A notable recent development is the Timed Racing Diffusion Model (TDRM), which combines a diffusion mechanism to account for the build-up of relative evidence, and a second component which triggers responses which may be taking too much time (Hawkins & Heathcote, 2021; Tillman et al., 2020).

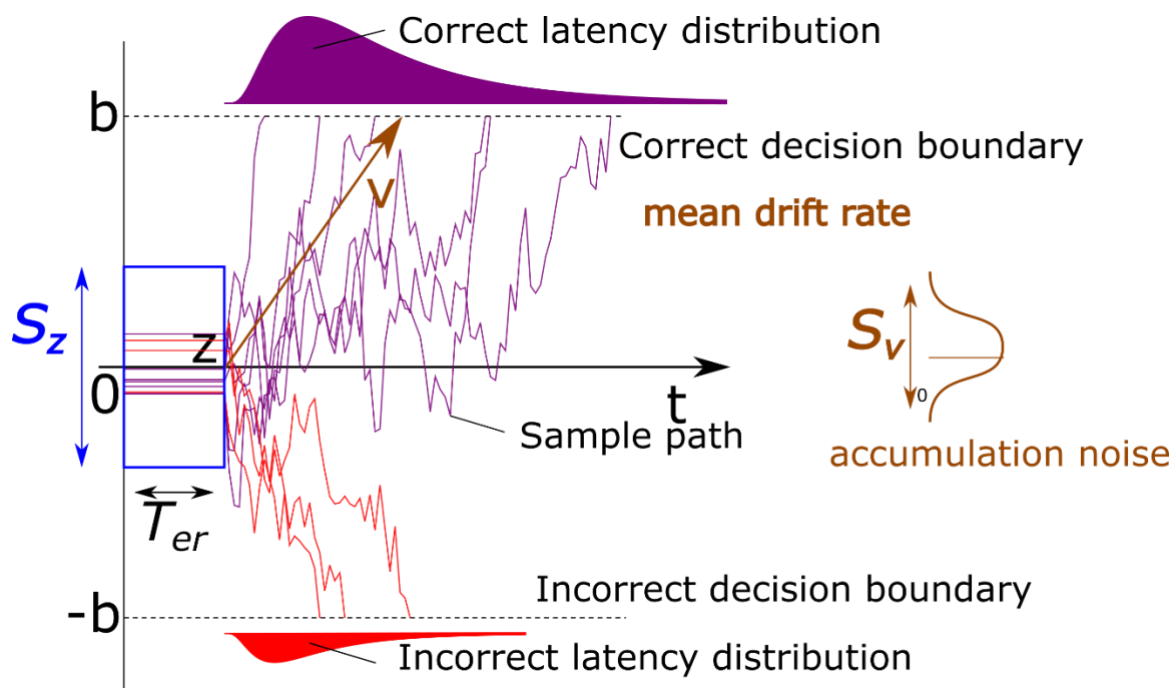
Overall, the simpler drift diffusion model has been the most popular model in recent years and is appropriate to use to explain tasks with binary response options. It forms the basis of the models developed by Resulaj et al (2009) and Lepora and Pezzulo (2014) to account for temporally extended actions. The work in this thesis (Chapter 4) builds upon this work, in particular the model of Lepora and Pezzulo (2014).

The basic structure of the drift diffusion model suggests five parameters which can in total account for the latency distribution of correct responses and the rate and latency distribution of error responses in two alternative forced choice (2AFC) tasks. As can be seen in the example paths in Figure 1-1, a decision variable accumulates information about the stimulus until a decision boundary is reached. At either side of the evidence accumulation stage (shown only before the accumulation process) there will be some **non-decision time,  $T_{er}$** . This time represents the minimum necessary time for transduction of the sensory information, and the time required to program and execute the motor response (this can also vary; Ratcliff &



Tuerlinckx, 2002). Once the stimuli have been encoded the decision process starts and evidence is accumulated at some **drift rate,  $v$** , proportional to the strength of the evidence. Noise is added to the accumulation process by the **drift rate variability** parameter,  $s_v$ . Early models (Ratcliff, 1978) assumed that the accumulation usually started from zero evidence, but by including **starting point variability,  $s_z$**  fast errors can be modelled. Finally, the **decision boundary separation,  $b$** , sets the level of evidence required to trigger the preparation of a response. For a given set of parameter values the proportion and reaction times of correct and error responses can be computed and compared to empirical data (Lerche & Voss, 2016).

Figure 1-1 Schematic of the Drift Diffusion Model of Decision-Making



Note. The figure shows the parameters of the drift diffusion model with example random walks demonstrating correct decisions (in purple) and incorrect decisions (in red). See text for explanations of each parameter.

### 1.1.3 Interpreting drift diffusion model parameters

Each of the parameters mentioned in the previous paragraph may be interpreted in terms of the underlying cognitive processes. The validity of such interpretation can be investigated using tests of selective influence. In a test of selective influence, one task parameter is manipulated at a

time in a way that should lead to a change in *one* specific model parameter. Manipulating task parameters will lead to changes in accuracy and reaction times. These data are then fit with the model, where one or more parameters are allowed to vary between the different task conditions. A successful test of selective influence shows that the effects of the experimental manipulation are best accommodated by the model parameter that was selectively targeted (rather than by a different parameter or combination of parameters). For example, Ratcliff and Rouder (1998) manipulated both the instruction (to respond either accurately or quickly) and the difficulty of a brightness discrimination task. When drift model parameters were recovered from the empirical data, the instruction manipulation changed the height of the response threshold ( $b$ ), and the difficulty manipulation changed the mean drift rate ( $v$ ), with little influence on the response threshold. Similarly, the starting point for the evidence accumulation process can be influenced by changing the relative frequency or the reward for each alternative in a 2AFC task (Leite & Ratcliff, 2011; Mulder et al., 2012; Ratcliff & McKoon, 2008). Non-decision time has been selectively increased by changing the response modality from saccadic eye movements to button-presses (Ratcliff & Tuerlinckx, 2002).

The processes for perceiving stimuli, reaching a decision and then programming a response are implemented across networks of brain areas. If decision-making was implemented as evidence accumulation to threshold we would expect neural signatures of: a) momentary evidence to be signalled by sensory units tuned to the task-relevant visual dimension, b) downstream units that integrate this evidence over time, and c) responses to be triggered when the integrated evidence reaches a threshold firing rate. Investigations into neural correlates of evidence accumulation often use a motion direction discrimination task with random dot kinematograms (RDKs) as the stimuli and saccadic eye movement as the response (Gold & Shadlen, 2007).

#### 1.1.4 Neural signatures of evidence accumulation

The momentary evidence used in a motion-discrimination task is the motion of a dot in an RDK. Along the visual processing pathway, it is neurons in the medial temporal (MT) or V5 area which detect motion (Newsome et al., 1989). Each MT neuron is being fed the activity of a larger number of lower-level feature detectors, so the retinal receptive field for an MT neuron is relatively large (Richert et al., 2013). For a typical RDK in non-human primate research it will be the combined activity of multiple MT neurons which drive the decision process (Trenholm & Krishnaswamy, 2020). MT neurons are each tuned to preferentially fire to certain directions of motion, so it is this information which must be accumulated somewhere for a decision to then be made. Shadlen and colleagues (for a review, see Gold & Shadlen, 2007) have hypothesised that the decision variable in a perceptual decision-making task (random dot motion discrimination) is accumulated in neural circuits involved in planning the motor action with which the outcome of a decision is signalled. For instance, when the direction of motion is indicated with a saccadic eye movement, it is neurons in the lateral intraparietal area (LIP) which appear to integrate sensory evidence coming from MT (Britten et al., 1992). Mazurek and colleagues (2003) tested this idea using a computational model of the decision process which used timing delays and spike rates from recorded data in area MT: Leaving only the decision threshold as a free parameter to be fit to the data, very close similarities were found between the accuracy and response timing of the experimental data and the prediction of the model. Similar ramping activity has been seen in other structures involved in the planning of eye movements which are themselves downstream from the LIP, such as the Frontal Eye Fields (Hanes & Schall, 1996) and Superior Colliculus (Ratcliff et al., 2007).

As well as areas related to saccadic control, activity has been observed in prefrontal or parietal cortices to tasks requiring saccadic responses to RDKs (Churchland et al., 2008; Kiani et al., 2014). Ramping neural activity has been seen the premotor cortex when the required response

to motion stimuli is a reach of the arm, rather than a saccade (Thura & Cisek, 2014). It is notable that in these studies the firing rate directly preceding a response did not depend on either the strength of the stimulus or the response time, supporting the idea of an activity threshold which is consistent across trials (Purcell & Palmeri, 2017). Overall, invasive neurophysiological studies find multiple locations which mirror evidence accumulation in the primate brain, which has prompted the search for similar activity in human subjects (Kelly & O'Connell, 2015).

In humans source localisation of EEG signals have been found to correlate with a build-up of sensory evidence in multiple areas at once (Philiastides et al., 2014), supporting the idea that decision-making activity is distributed across multiple regions. If there are general mechanisms like evidence accumulation implemented in the brain, the magnitude of blood-oxygen level dependent (BOLD) signals may correlate with the strength of evidence for one stimulus over another. Heekeren et al. (2004) found this in a task where participants had to choose whether an image was a house or a face each of which were corrupted with various amounts of noise. When the stimulus was clearly a face, there was high activity in face-selective areas of the ventral visual cortex anticorrelated with activity in the house-selective areas, and vice versa. When the stimulus was a noisy image of either a face or a house, lower activity was seen both house- or face-selective areas, while regions which correlate with attentional effort increased in activity. For this task, an area in the dorsolateral prefrontal cortex (DLPFC) was found to be more active when evidence was stronger for either houses or faces and, like an accumulator, also correlated with the difference in activity between the object selective areas as the trial progressed.

To summarise, it seems highly likely that categorical perceptual decisions are computed by a process of noisy evidence accumulation to a boundary. The accuracy and response time of a task can often be comprehensively modelled by evidence accumulation models, and both single unit recordings and brain imaging provide neural signatures of evidence accumulation. The precise

location of decision-making, or even where evidence is accumulated, appears to have signatures in multiple brain areas, at least some of which are motor areas which are active during response (Thura & Cisek, 2014). This idea opens the possibility that the decision related activity not only feeds into the *planning* of the motor response, but potentially also in its *execution*. In other words, the final stage of the decision-making in an evidence accumulation framework, motor execution, may be involved in the decision process rather than merely the expression of an entirely resolved decision. How these areas are functionally related as they contribute to the perception-cognition-action loop needs examining.

#### 1.1.5 The loci of decision and action

Given that evidence accumulation processes appear in multiple places, a related question to *where* task-relevant decisions are computed is one about the overall hierarchical organisational of decision-making systems and whether any single location can meaningfully occupy the apex of such a hierarchy. Traditional views suggest that there may be a central domain-general area for making decisions, such as the DLPFC, where all comparisons relevant to the task are made, whether they be comparisons of sensory evidence, hedonic value or subjective utility (Ho et al., 2009). A highly serial version of such a view would suggest that activity upstream from this central decider (which apparently correlates with an accumulator) would merely be feeding information to that area, while apparent accumulators downstream from this area would be just resonating with that central activity.

Alternatively, multiple accumulation signals may be distributed across multiple neural circuits in parallel, all of which contribute to the process of deciding and acting. As mentioned above, for example, Heekeren et al. (2008) proposed that rather than the traditional serial process, sensory evidence flows in parallel to premotor areas, motor areas and into decision calculations in the DLPFC, yet with no particular information stream having primacy in the organism's decision-making process. Here, so-called "domain general" decisions are made between ongoing

alternative perception-action couplings – the “evidence” (and correlated activity) for one choice over another distributed across that coupling.

The strong versions of embodied cognition go even further: neural decisions are made by a distributed consensus, and the location of a neural activity shifting the organism from one particular course of action to another is not in a domain-general, ultimate decider, but dynamic, embodied, and embedded in the organism’s environment (Cisek, 2012). So, if a decision requires pushing a lever to the left or the right why not “make” the decision in the area of the brain where the leftward or rightward motor responses are prepared, while the very high-level decision of whether to continue participating in the experiment or to leave the lab would be accumulating somewhere else like the DLPFC. In this formulation, motor areas are primal for motor decisions (and perhaps more so for over-trained non-human primate subjects) while for more novel sensory or less straightforward decisions other brain areas reflect best the locus of evidence accumulation and decision.

Whichever the case, it seems clear that motor areas are involved in the kinds of decision processes required by most lab-based experiments, either primarily, secondarily, or as part of a diffuse consensus mechanism (Cisek, 2012). Should a particular decision require triggering one of two motor options, both of these may be generated and decided between (Cisek & Kalaska, 2010). A window into decision processes before choices are made may be available by tracking movements made in response to a decision, rather than just the response time and accuracy of that decision.

Evidence accumulation models have been extended to far more than simple perceptual decisions. In principle, any decision between competing options involved an accumulation of evidence (Ratcliff et al., 2016), whether it’s a lexical decision (Anders et al., 2015), food choice (Sullivan & Huettel, 2021) or social decisions (Krajbich et al., 2015), and even how stereotyping may influence the decision to shoot somebody (Pleskac et al., 2018). All previously discussed

examples of research like this, have, however, depended on “ballistic” outcomes like button presses or saccades, that offer no opportunities for expressing nuance or revision. A much-vaunted technique to examine more closely how decisions are made has been through the use of process-tracing methods, including mouse tracking (Schulte-Mecklenbeck et al., 2017).

## *1.2 Moving beyond the pushing of buttons to record responses*

So far, when discussing the behavioural response to a decision, most measurements have been recorded at the endpoint of a decision be it spoken out loud, the action of pressing a button, or making a saccade to a particular location. These outcomes are regarded as “ballistic”, in that once they are triggered, they are set into inevitable motion. Other kinds of response are not so ballistic in that they may be halted or modified during the action. Process tracing in psychological research claims to overcome this limitation and encompasses any technique that records measurements continuously during a task, and as such includes movement data as well as eye tracking, skin conductance, EEG, fMRI and verbal reports from before a decision is made (Schulte-Mecklenbeck et al., 2017). For example, information acquisition leading to a choice can be tracked using eye movements with the number and duration of fixations correlated with preferred choice (Russo, 2019). Whilst individual saccades are often the archetypal ballistic response – they rapidly shift focus from one location to another in a usually straight line – curved movements, possibly reflecting competing movement plans in the superior colliculus (SC), have also been observed (Van der Stigchel et al., 2006).

Hallmarks similar to response competition in the superior colliculus driving curvature in eye movements have been measured in reaching tasks in the dorsal pre-motor cortex and primary motor cortex (Cisek & Kalaska, 2005). In several experiments, the authors show that when a subject has to decide between several reaching targets (e.g. based on value; Pastor-Bernier & Cisek, 2011) action plans for multiple options are generated in parallel, and this activity correlates with decision variables are distributed across a diverse range of cortical areas (Cisek &

Kalaska, 2010). If competition between these plans is not fully resolved when movement is initiated, reaching movements may have the potential to show more complex competition than saccades. The intermediate locations occupied during a reach action could then be a very direct reflection of the state of the decision variable while the decision is being made (Freeman, 2018).

#### 1.2.1 Response competition in mouse movements and their measurement

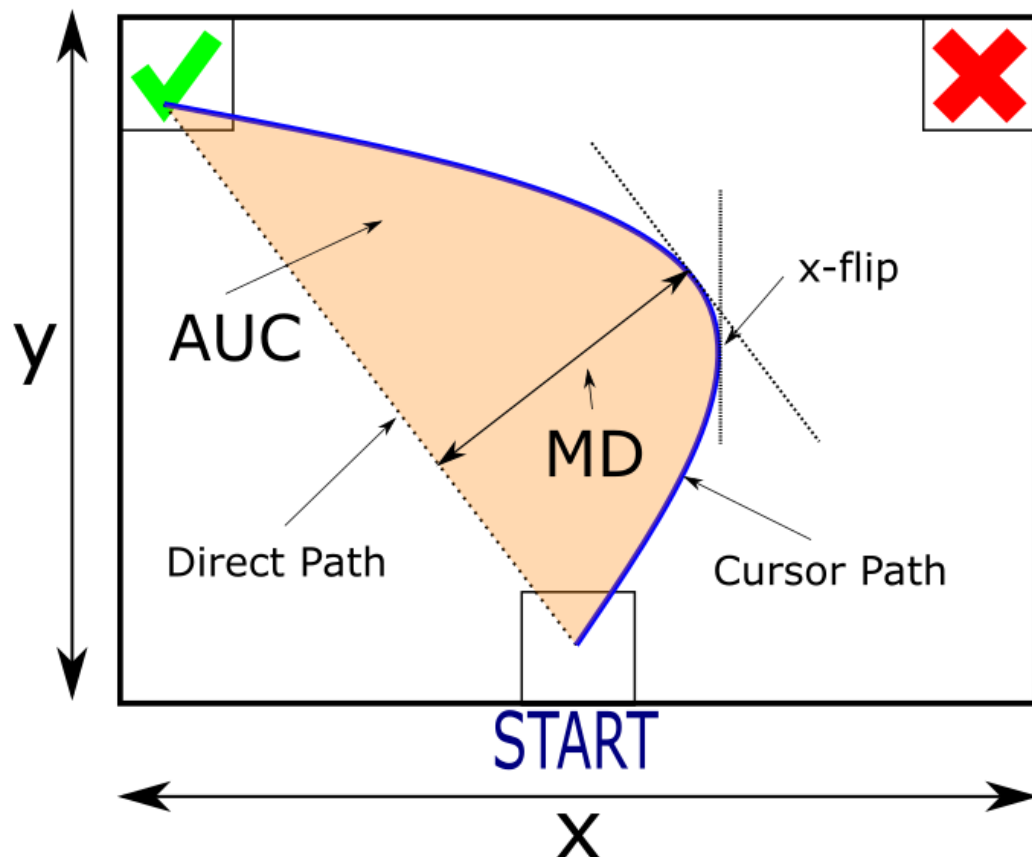
This assumption that trajectory deviations during reaching reflect the “microstructure” of decision-making is foundational mouse tracking research (Freeman, 2018). The evolution of these research methods has followed the advent of the computer mouse which can allow inexpensive access to hand location data with relatively precise temporal and spatial resolution (Phillips & Triggs, 2001). There are now many studies which have used mouse tracking for a variety of research problems where parallel or dynamic processing theories are being tested against stage-based or serial models of processing. You may have a theory that social judgements are a mix of fast, stimulus driven, heuristic or intuitive judgements, and slower, controlled, rational and deliberate judgements (Kahneman, 2013). In such a task both decision systems may start at the same time, but the “fast” process naturally resolves first and initiates movement the intuitive response. However, if the “slow” judgement later comes to a different conclusion the initial choice now needs to be overridden. The resulting mouse trajectory will show a rapid initiation to the “wrong” target and a subsequent change of mind. On the other hand, you may have an alternative theory which suggests only one dynamic decision system, and as competition between the response options or their motor plans gradually resolves, the resulting mouse trajectory is a sinuous curve as evidence builds for one option over another.

An example of a mouse tracking study into dynamic decision-making is that of Schneider and colleagues (2015) who asked participants to move their mouse from the bottom centre of the screen to the top-left or top-right to indicate whether they had a positive or negative attitude towards a stimulus. Stimuli were either unambiguous (e.g., happy, holiday, depressed, disgust)



or ambivalent (e.g., organ donation, alcohol). As may be expected, greater curvature was found for the ambivalent stimuli. Schneider and colleagues summarised the curvature of each mouse trajectory was its maximum deviation (MD), calculated as the greatest difference between the trajectory and an ideal line from the start-point to the end-point (see Figure 1-2), and the time at which the MD occurred. Both measures were averaged over stimuli, trials and conditions. A similar measure to MD is the area under curve (AUC), which as the name implies is the area between the direct path from the start position to the response and the actual trajectory. Another common measure is the x-flip, where the cursor reverses direction in the x-axis. The number of x-flips may be used as an index of vacillation between response alternatives. If there is no competition in the movement plans, or the evaluation is always completed before movement initiation, then there would be no “attraction” to the unselected option, even when (as was the case) overall response times for ambiguous stimuli were longer than for the unambiguous stimuli.

Figure 1-2 An Example of the Typical Set Up of a Mouse Tracking Study and Trajectory Measurements



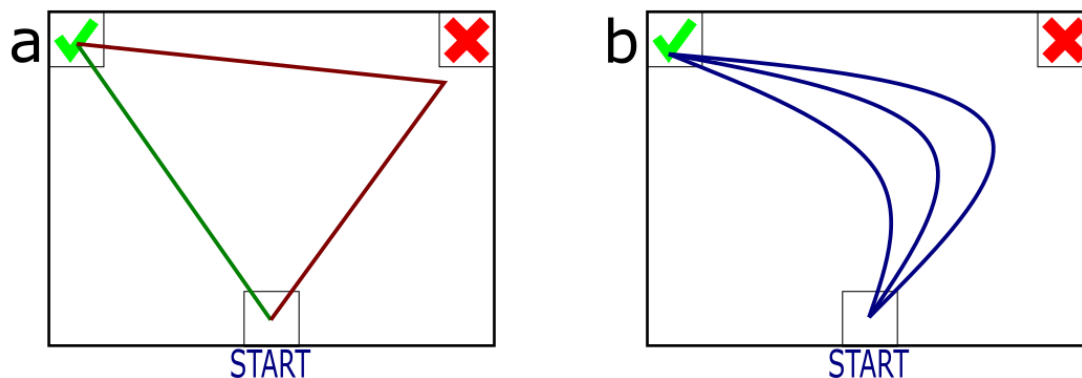
*Note.* Diagram shows how summary measures are often calculated from mouse paths. In the diagram the “correct” target is in the top left, with the “incorrect” in the top right. The mouse cursor will begin the trial at the start location. The blue line is the trajectory of the mouse cursor as it selects the correct target while experiencing “attraction” to the incorrect target. The Direct Path is the ideal trajectory should no attraction have occurred. The maximum deviation (MD) is the largest single distance between the trajectory and the Direct Path. The Area Under Curve (AUC) is the area between the trajectory and the direct path. The x-flip is the point at which the movement in the x-dimension changes.

### 1.2.2 Using trajectory information to find evidence of dynamic decision-making

As mentioned above, often these studies pit dynamic processing theories against stage-based or dual process theories. Any cognitive process which may be comprised of multiple processes (operating in parallel or serially) would likely generate trajectories which switch targets as option B replaces option A (Freeman & Dale, 2013). In contrast, dynamic processing will generate trajectories that all curve to a degree determined by the progression of ongoing stimulus processing. The strongest version of the dynamical systems approach was put forth by Spivey (2008) who suggested that mouse trajectories can be an expression of the “pull” and “push”

between attractors and repellers, each of which accords to a response. In less ambiguous trials there will be an overwhelming pull to the correct option and repulsion from the incorrect option, while on more ambiguous trials these forces will be more balanced, much like Cartwright & Festinger's (1943) concept of “driving forces” but now these forces are embodied in the movement itself, and measurable by researchers.

Figure 1-3 Schematic of Potential Trajectory Types in either a Dual Process or a Dynamic Process



*Note.* a) Simplified mouse paths from a serial process where the initial decision is correct (shown in green) or the initial decision is revised by a slower process in a discrete change of mind (shown in red), note that real trajectories would have some curvature in the direct case, and no “sharp” change in the change of mind trajectory; and b) trial paths which show ongoing competition between response options and continuous changes of mind any varying attraction to the incorrect response.

Testing for bimodality of trajectory curvatures within a condition is often used to judge whether the response dynamics are more likely to reflect a the results of a dual process or a single, dynamic process (Freeman & Dale, 2013). As can be seen in

Figure 1-3(a), a condition where mouse trajectories are mostly either straight, with no movement towards the incorrect response, or initially a relatively large movement to the incorrect response which is then revised will show a clear bimodal distribution of curvatures. However, if mouse trajectories are generated by ongoing competition, as in

Figure 1-3(b), and all trials exhibit some level of “attraction” to the incorrect response it is assumed that distribution of trajectory curvatures will be unimodal. A variety of statistical tests exist for bimodality and were assessed by Freeman and Date (2013), but none are free from bias, and bimodal response distributions may be more likely under certain design constraints, rather than evidence for a particular theoretical stance on the nature of cognitive processing. If researchers do not check for bimodality, then analyses based on an aggregation of the data may lead to misleading conclusions.

### 1.2.3 Dynamic decisions as an artefact of trajectory averaging

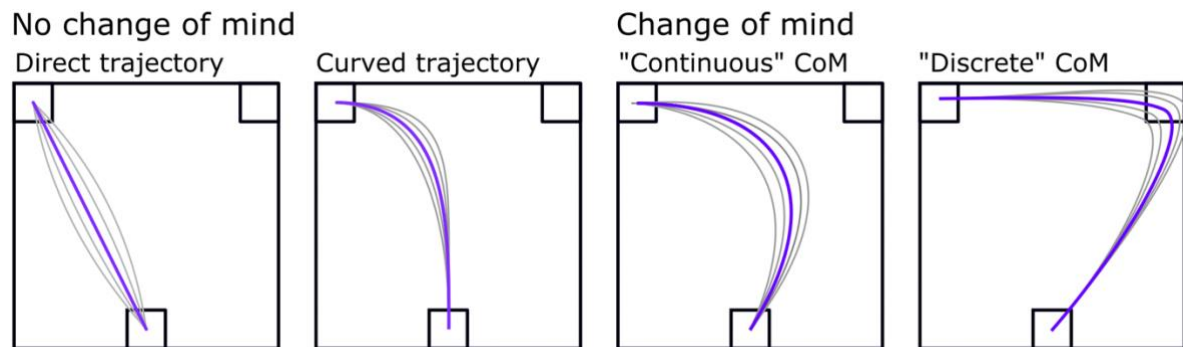
The difference in curvature between averaged mouse trajectories has been used as evidence that complex judgements are formed gradually. These judgements are usually the categorisation, via mouse cursor, of ambiguous versus less ambiguous stimuli such as faces with “androgynous” features in comparison to more clearly gendered faces (Freeman et al., 2008), or words which share initial phonemes (Spivey et al., 2005) and even how “true” a contentious statement such as “murder is sometimes justifiable” may be (McKinstry et al., 2008). Frequently analyses are conducted on some averaged summary measure of the trajectory like MD or AUC, on the basis that the judgement of an exemplar into category A or B does not involve a qualitatively different process, unlike a Stroop task (Bundt et al., 2018; Kimura & Nakano, 2021), for example. Averaging summary measures over conditions effectively assumes and that dynamic competition exists in all trials and the average trajectory will be representative of the typical response. The dual-system alternative is that some trials may go directly, without conflict, to the response option while some go initially to the incorrect option before being corrected during the movement (Freeman, 2018). Mouse trajectory data with a unimodal distribution of curvatures are assumed to reflect a dynamic processing system, while mouse trajectory data with a bimodal curvature distribution are assumed to reflect a dual-process

model (Schulte-Mecklenbeck et al., 2019). But, as will be discussed below, the shape of response distributions can be strongly influenced by study design.

#### 1.2.4 Dynamic decisions as an artefact of study design

When using mouse trajectory information to judge between dynamic or dual processing models there are simple design factors that have an influence on the results of these studies, which can lead to different conclusions. Kieslich et al., (2020) investigated how common mouse tracking effects changed with study design. These design factors were manipulated in the study which used identical stimuli from Dale et al. (2007) where participants had to categorise an animal into its correct class. For example, “Mammal” and “Fish” were presented as response options and a typical exemplar (e.g. “cat”) would be easily classified, and an atypical animal (e.g. “whale”) would be expected to show deviation. In addition to aggregating curvature metrics across conditions, Kieslich et al. categorised trajectories according to their similarity to several “prototype” trajectories: direct trajectories, curved trajectories, continuous changes of mind, and discrete changes of mind (see Figure 1-4). The direct trajectories simply move straight from the start to the response. The curved trajectories may have some slight “attraction” to the alternative response, but not enough to cause an x-flip. Continuous changes of mind are also smoothly curved along their length, have an x-flip due to significant “attraction” from the alternative response, before smoothly curling back. Discrete changes of mind travel more or less directly towards the alternative before a sudden shift before or on the alternative response option.

Figure 1-4 Example of Trajectory Prototypes from Kieslich et al. (2020)



*Note.* Each “prototype” trajectory (purple) is used to categorise recorded mouse trajectories (simplified examples in grey) using a clustering algorithm. Trajectories without a “change of mind” may be direct or curved, and trajectories with a change of mind may shift continuously, or discretely from one target to another. Figure is a re-creation based on the published work by Kieslich et al. (2020).

Using this system of comparing trajectories to prototypes, as well as the more usual

aggregations of curvature metrics, Kieslich et al. (2020) demonstrated that decreasing the speed and disabling acceleration of the mouse cursor lowered maximum deviation measures for both typical and atypical stimuli. However, this was mostly due to a higher proportion of discrete change-of-mind trials in both conditions. When changing the requirement to indicate a response with a mouse click, to one where the participant just moved the mouse cursor over the response region, decreased aggregate MDs by virtually eliminating discrete change of mind trajectories.

Notably, this modification also altered the distribution of MDs from bimodal to unimodal.

Altering the trial starting procedure resulted in changes to the relative proportions of trajectory types for otherwise identical cognitive tasks. That is, compared to the condition in which stimuli were visible from the start of the trial and no time pressure was applied, asking participants to start moving early in the process, or only displaying the stimulus when participants had begun to move the mouse cursor, increased deviation for the “atypical” condition and dramatically reduced “straight” responses overall. Furthermore, requiring rapid initiation or obscuring the stimuli until movement onset led to a large number of trials where participants pushed the mouse straight up. Until the work by Kieslich and colleagues (2020) it has been assumed by most researchers that aggregating trajectory curvature is a sufficient analysis of mouse tracking data,

so long as the curvature distributions meet some criteria for unimodality (Freeman & Dale, 2013). It is worth noting here that the Kieslich suggest that the mapping between the cognitive process and the movement may be what is changed by this manipulation, not the nature of the cognitive process itself. Thus, as will be discussed below, the design choices of a mouse tracking study may lead to a static decision process generating dynamic shifts in movement, or the converse, where a highly dynamic underlying decision process will generate movements which express none of that dynamicity.

#### 1.2.5 How dynamic is it really?

There is now a large body of research that has operated under this assumption that mouse-tracking can reveal something more about the unfolding decision processes than a simple button-press response (Stillman et al., 2018). That idea that the gradual unfolding of a decision can be tracked directly is intuitively appealing when considering that the brain is composed of networks of neural activity with multiple parallel connections from one area to another (Spivey & Dale, 2006) and has been a cornerstone of the mouse-tracking literature into high level decision-making (Freeman, 2018). In addition to the studies mentioned above, mouse tracking has been used to investigate self-control and conflict in food choice (Georgii et al., 2020; Ha et al., 2016; Lopez et al., 2018; Pearce et al., 2020; Stillman et al., 2017), numerical cognition (Faulkenberry et al., 2018; Fischer & Hartmann, 2014; Marghetis et al., 2014; Moeller et al., 2009; Song & Nakayama, 2008), social cognition (Melnikoff et al., 2021; Smeding et al., 2016), executive control and bilingualism (Incera & McLennan, 2018), attempts to detect socially desirable responses in personality measures (Mazza et al., 2020) and even lie detection (Monaro et al., 2017). While for many of these studies it may be sufficient to simply compare the MD, AUC or number x-flips between one experimental condition and another and treat that only as a signal of increased conflict during decision-making. However, the assumption that the dynamics of mouse trajectories reflect the dynamics of the underlying decision process is typically implicit.

Where the assumption is made explicit, authors often do not specify what this link involves beyond invoking the theoretical stance taken by the proponents of embodied cognition and citing the neurophysiological work of Cisek and Kalaska (2005), or their successors.

Furthermore, in mouse-tracking studies it is very small movements of the fingers and wrist are translated into large movements of the mouse cursor. Dynamic shifts in cognition are inferred from cursor trajectory shifts, but the theoretical underpinning for the link between decision-making and movement is from the whole-reach tracking from Cisek and Kalaska (2005). The differences between moving a mouse cursor and moving one's arm and hand include that larger muscles are needed to be activated to move the whole hand for a reach movement, rather than just the fingertips, the motion itself is in three dimensions rather than constrained to a plane, but despite this, reaches (relative to mouse cursor aiming) are initiated faster, and also respond faster and with greater curvature when the target is displaced (Moher & Song, 2019).

As outlined earlier, there is a history of success in decision-making research using evidence accumulation models, and such models are frequently claimed to be the neural basis of all decision-making processes (Schall, 2001). However, since these models have been developed with saccade or button-press responses, all decision activity is regarded as finished at movement onset and has no further part to play. In contrast, mouse-tracking paradigms assume a degree of interconnectedness between the decision and the motor output. As will be described below, such a tight coupling between cognitive processing and ongoing behaviour may not be so straightforward.

### *1.3 The control of reaching movements*

To aid in the application of these insights to movement trajectories under choice conditions (perhaps to aid psychological process tracing) a brief tour of motor control is presented below. All movements contain some variability, and the field of motor control has moved from mere descriptions of the movement characteristics (i.e., the variability of movement initiation latency,



movement speed, and accuracy) to neural explanations and modelling and of such phenomena (Rosenbaum, 2010). Accounting for the different types of trajectories found in (e.g.) mouse tracking studies, will differ according to how the internal decision is modelled, the way that the motor system is linked to those decision processes and potentially confounded by the strategies that any participant may employ to perform well according to task demands.

### 1.3.1 The planning and execution of direct goal-directed movements

Explanations of the kind of point-to-point movements which make up the direct mouse movement paths have been extensively studied since the 1980s (Jeannerod, 1988; Rosenbaum, 2010), though investigations into what factors influence movement accuracy have a long history in psychological research (Woodworth, 1899). The most fundamental characteristic of reaching movements is the relationship between the time the movement takes, the distance that movement must traverse, and the size of the target object, known as Fitts' law (Fitts, 1954). The law holds under most circumstances for the free movement of a stylus gripped in the hand in Fitts' original work and for the movements of a mouse cursor in later work (Radwin et al., 1990). Most reaches towards a single static target will tend to be straight (or slightly curved) with a "bell shaped" velocity profile. This is a symmetric velocity profile which rises smoothly to a maximum before smoothly decelerating until it has stopped (Suzuki et al., 1997). An increase in time pressure for the overall reach tends to increase this symmetry, however high accuracy demands may also extend the deceleration phase (Klein Breteler et al., 2002; Milner & Ijaz, 1990).

The achievement of a geometrically simple movement of the hand requires rather a perhaps surprisingly complicated routine of joint rotations, extensions and flexions (Morasso, 1981). Furthermore, that the *same* direction and velocity profile of the end-effector (hand, tool, or mouse) can be achieved by a theoretically infinite set of sequences and strengths of muscle activations, but typically are not, perhaps indicates that it is the hand trajectory which is

generated first, and then the “inverse kinematic problem” is solved to decompose the movement into motor neuron signals. Research consistently indicates that movement planning is done at the end-effector level (such as the hand or tool-tip) as these plans are decomposed into commands to contract muscles via direction-specific population codes in the motor cortex (Georgopoulos et al., 1986).

Suggestions on how this problem is efficiently solved typically involve taking the movement goal for the end effector (e.g. move the hand from one position to another) and then calculate an optimal movement plan to minimise some kind of cost function, perhaps one minimising the rate of change in acceleration, termed jerk (Flash & Hogan, 1985), the torques applied to each joint (Klein Breteler et al., 2002), or the variability of the final position (Harris & Wolpert, 1998). These investigations only refer to the “planning” phase of the movement (at least under the “classic” view of human motor control), and are never perfectly executed due to inherent variability at every stage (Harris & Wolpert, 1998; van Beers et al., 2004). Compensating for this inherent variability is essential for successful movement. As repeated practice naturally refines the accuracy in movement planning and movement initiation (Shadmehr & Mussa-Ivaldi, 1994), fine-tuning a movement in response to feedback is a critical part of motor control (Rosenbaum, 2010).

It's important to point out here that the field of optimal motor control has not come to an agreement about which cost function is being optimised (Friston, 2011; Guigon et al., 2008). Indeed, it is frequently suggested that the true cost function for any particular movement in any particular task may be a combination of costs functions (Schaal et al., 2007). For example, some cost function for optimising speed will usually be in opposition to a cost function for accuracy (the classic speed-accuracy trade-off), but both will be constrained by a cost function which minimises the risk of injury, perhaps via limiting joint torque or movement jerk. Whichever single or multiple cost function is used to plan a movement, a system for motor control needs first to

translate a movement goal into a movement plan before transforming that plan into the desired impulses, while simultaneously adjusting that plan if the external environment or the goal changes (Todorov & Jordan, 2002). While the initial planning is executed by a *forward controller*, adaptation of ongoing actions is achieved by a *feedback controller* comparing visual and proprioceptive input to an efference copy of the action. The efference copy is a prediction (or simulation) of the visual and proprioceptive consequences of the planned action, and differences between these two can be rapidly transformed into corrective commands. Optimal feedback control theory is currently the dominant paradigm in human motor control (Merel et al., 2019), and is an elegant solution to the degrees-of-freedom problem which concerns itself with the computations necessary to support flexible goal-directed movement.

Dynamical Systems Theory presents an alternative ecological explanation wherein the motor system only needs to set a new equilibrium point or reference configuration, and let the muscles and tendons of the musculoskeletal system sort out the rest (Latash, 2012). In this formulation there are no cost functions, per se, but the apparently optimal control behaviour is instead an emergent property of neural dynamics and the physics of movement. If the organism has the goal of moving their hand from one location to another, the coordinates of the desired location become an attractor basin in the ongoing dynamics of neural activity in the motor system (Erlhagen & Schöner, 2002; Knips et al., 2017). This shift induces a difference between the expected proprioceptive feedback and the actual feedback received from the limbs, which is resolved by contracting some muscles while others are relaxed. Furthermore, in this view the variability of motor actions isn't always from sub-optimal stochasticity in the motor planning process, but a natural consequence of neural dynamics in which there is a region of equivalent performance (Martin et al., 2019). Movement planning is thus the activation of new reference configurations, and motor control is thus the process of moving from one equilibrium point to another across a manifold of equivalent solutions (Sainburg, 2015), not a series of intensive computations.

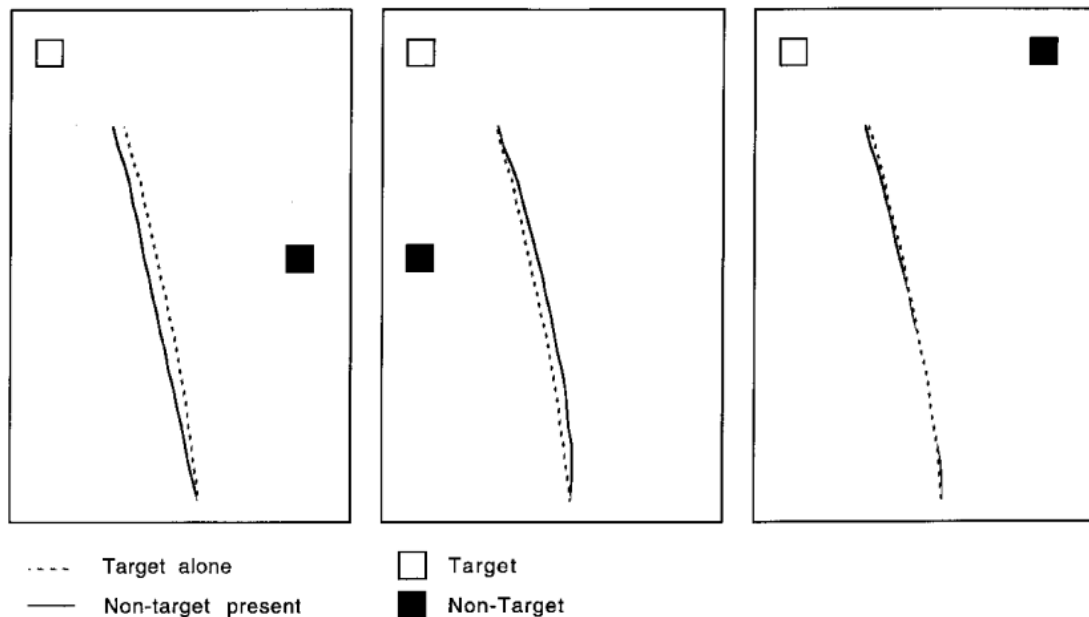
Even for simple pointing actions the symmetrical velocity profile of a reach, as may be expected from a ballistic action, breaks down in tasks where extreme accuracy is required (Milner & Ijaz, 1990), as well in reaches-to-grasp where appropriate finger placement is crucial (Jeannerod, 1988). From these studies there is some evidence that the control of movement may not be continuous, which has implications for any assumed direct link between cognition and action as suggested by the mouse-tracking literature. For example, when reaching to place a peg into a narrow hole under time pressure, secondary corrective movements are not continuous but occur intermittently at about eight times a second (Gross et al., 2002). As well as extending the latter part of the reach for difficult aiming movements, when participants were asked to slow their reach down so that a movement of only a few centimetres took around a second, the entire movement was seen to proceed in fits and starts with the same rate (Milner & Ijaz, 1990). Similarly, when engaged in a continuous motor task, such as balancing a pendulum, slower rates of corrective movement are observed (Loram et al., 2006). These small movements are termed “submovements”, and by themselves considered to be unmodifiable once triggered. Reasons for the limited rate are unclear but may be due to oscillatory activity in the brain or a refractory period neural signal generation, muscle response. The picture is further complicated by the possibility that intermittent motor control may be able to mimic continuous control when distinct submovements at the level of muscle activations overlap at the effector level (Gawthrop et al., 2011).

A straight movement to a single target may tell us little about the underlying decision process that a button-press response will not, however experiments which evoke curved reaching trajectories may be linked with more explicit decision-making processes. Before we deal with that, it is necessary to review how the motor control literature has investigated and understood the generation of curved reaching movements.

### 1.3.2 The planning and generation of curved goal-directed movements

Distractor-interference effects may provide some evidence that curved reaching movements are the result of the parallel specification of multiple movement plans (Tipper et al., 1997). Contrary to the averaging of trajectories seen when multiple targets are present, there is sometimes curvature away from the distractor, even in conditions in which the distractor is not an obstacle to the movement itself. Tipper and colleagues (1997) tracked the fingertips of their participants and asked them, on a cue, to reach for and grasp a 30mm cube of wood which could occupy any location in the four corners of a square, along with occasional no-go trials. Participants faced one side of the square with their hand on the midline several centimetres outside of the square. In some trials there was no non-target object, and these trajectories were compared with trials in which a non-target was present. Additional experimental manipulations included allowing the participants to select the target long before the movement cue, or a simultaneous target cue and movement cue but with 1-2s to view the object locations, or restricting total viewing time of the stimuli to 300ms before the movement cue. No deviations were seen with the least restrictive viewing and movement criteria. As time for target viewing was increasingly restricted, slight trajectory deviations away from the non-targets were observed, even when these were not obstacles. This effect was most extreme when participants had very little time to view, select and reach for the target. In accordance with evidence that direction-sensitive motor cortex neurons decrease their firing rates below baseline when reaching in the opposite direction (Georgopoulos, 1990), Tipper and colleagues (1997) proposed that multiple motor plans were generated when the targets were viewed, and under tight time conditions the action plan for the non-target needs active inhibition to prevent interfering with the desired action. Without this active inhibition, the motor plans will combine, and the hand may collide with the non-target.

*Figure 1-5 Wrist paths of reaches from Tipper, Howard and Jackson (1997)*



Note. Figure shows mean wrist paths recorded which deviated away from a non-target, despite the non-target not being an obstacle in the way of the reach action. Figure from *Selective Reaching to Grasp: Evidence for Distractor Interference Effects*, Tipper, Howard & Jackson, *Visual Cognition*, 4:1, 1-38, © copyright 1997, reprinted by permission of Informa UK Limited, trading as Taylor & Taylor & Francis Group, <http://www.tandfonline.com>

In contrast, Welsh et al. (1999) investigated distractor interference effects that showed curvature *towards* a distractor. In a later experiment they also established that the time between the appearance of the target and the distractor was critical to generating curvature either towards or away from the distractor (Welsh & Elliott, 2004). They suggested that there needs to be enough time for inhibition of the non-target response for it to “push” trajectories away, while movement triggered before that process can complete will lead to a pull towards the distractor due to mixing between the activated action plans. The trajectories recorded in a mouse-tracking task may then show trajectory averaging between motor plans (the classic “attraction”) only when task conditions require movement in advance of the inhibition taking effect.

### 1.3.3 The execution of movements to multiple targets

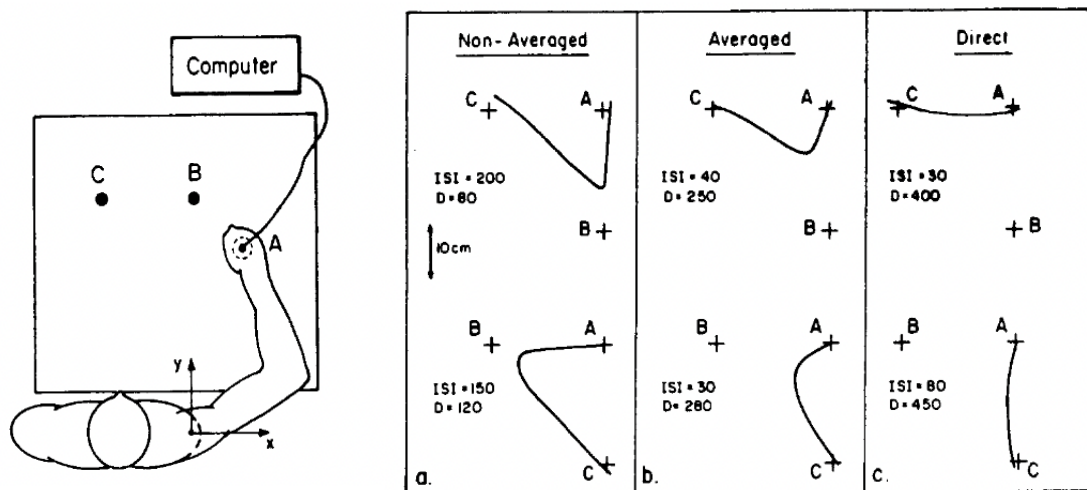
Flash and Henis (1991; Henis & Flash, 1995) conducted experiments that are reminiscent of deciding between pairs of action plans, only to later revise that movement to the initially

unchosen target. Very large curvatures of reach direction towards an (eventual) non-target are seen in double-step target-displacement experiments. Participants held a stylus on the surface of a table at a starting position (A). When the trial began, the target position (B) was illuminated and stayed lit on control trials, while for experimental trials the target was switched to a third position (C). The initial target location B was one of two equally probably locations, and the displaced target C could either be in the unused initial target location, or a third location. This switch could occur after an experimentally controlled delay from 10 to 300ms. In trials where no displacement occurred, direct path with a bell-shaped velocity profile was generated. Curved movements were elicited when the target switched between 10 and 100ms into the trial – initial trajectories were in an “average” direction towards a position between target positions A and B, perhaps due to a mixing of movement plans resembling a “continuous change of mind”. In trials where the target switched after 100ms, and often after movement initiation, the initial movement was unambiguously towards B before being revised, much like the “discrete changes of mind” seen in mouse tracking literature.

Using these results, Henis and Flash (1995) suggested that they could explain the recorded trajectories at the motor plan level through a superposition of movement plans. For the trajectories without averaging, i.e., those where the target displacement occurred more than 100ms after the trial start, the initial plan to move the hand from positions A to B is initiated without interference, but during the reach a separate motor plan is superimposed on this ongoing movement. The additional plan is one that should move the hand from position B, (the initial target) to C (the updated target). The resulting trajectory is a smooth curve which heads towards B at the start, and smoothly curves to C. For the trajectories where the target was displaced less than 100ms after trial onset the initial trajectory is longer towards the initial target, but to a blend of the target positions B and C. Henis and Flash suggested that there was still a superposition of two separate plans, but now the first is towards a blended target, and the superimposed plan moves the hand from the blended-target position to C. The blended-target

position is on the line between B and C, and its precise distance along that line is related to the time delay between the trial onset and the target updating time.

Figure 1-6 Experimental Set Up and Trajectories from Flash and Henis (1995)



Note. Left: experiment set up. Right: representative trajectories when either (a) stimulus displacement occurs shortly before the initial motor plan is triggered, so the corrective motor plan is superimposed upon the initial unmodified plan, (b) stimulus displacement occurs slightly earlier, modifying the initial plan with an average, and (c) stimulus displacement occurs long before the movement is initiated, and the trajectory is solely to the updated target position. Reproduced with permission from the publisher.

The Henis and Flash experiments suggest that that when faced with multiple potential movements these are prepared in parallel and may interact, as Cisek (2007) was to later support. Before each trial, the participant would generate multiple action plans, each a direct move to the potential initial target. During the task one of those plans will be selected, and if uninterrupted be executed without issue. However, after rapid target displacement both motor plans must still be occupying movement planning resources. Once a movement is triggered, the “new” motor plan does not have time to fully overwrite the initial plan, so an averaged trajectory is followed.

In Tipper et al. (1997) the action plan to the non-target was actively inhibited, and this mechanism resulted in reach trajectories that were warped away from the non-target, while in the Henis and Flash studies, neither action plan was inhibited, so the resultant initial trajectory



could show target blending. These studies are presented together here to highlight how curvature away and curvature towards non-targets have been seen in the kinematics of reaching and the occurrence of these will depend on the temporal relationship between trial start, target switching and movement initiation. In all so far, the participant will have been preparing for a movement to a single target, which may or may not be switched with another. The typical choice-reaching paradigm, however, often presents multiple targets on the expectation that selection will happen during the reach in a paradigm referred to as 'go-before-you-know' (Gallivan et al., 2015, 2018; Gallivan & Chapman, 2014).

In these experiments participants typically reach towards a screen on which a pair of targets are presented, without knowing which they will ultimately be asked to select until they are part way through the movement (Gallivan et al., 2015; Gallivan & Chapman, 2014). Once a target is cued participants will adjust their trajectory. The studies frequently claim that the early part of these trajectories reflects an efficient "co-optimisation" of the movement trajectories such that energetic costs are minimised until a point in the reach where target uncertainty has been resolved by the target cue. Should the agent be generating a movement plan for each potential target, they may be blending both to form the initial trajectory. Looking closer at trajectories with early "intermediate" paths, Wong and Haith (2017) varied the speed at which participants made reaches towards pairs of targets (with peak velocities between 0.3-0.7m/s for the slow trials, and 0.8-1.5m/s for the fast trials) and also varied the separation between the targets. As with most go-before-you-know tasks, the target cue appeared only when the fingertip of the participant was more than 25% of the way to the response screen. Slowing participants down and decreasing target separation caused participants to favour an intermediate (i.e., "co-optimised") trajectory, but under fast reaching conditions and when targets were further apart, participants mostly just switched from one target to another. These results called into question the idea that multiple interacting motor plans are the cause of intermediate reach trajectories, suggesting instead that strategic deployment of a single motor plan was sufficient to explain the

measured trajectories. The debate over whether it is multiple action plans that are decided between, or a single action plan applied to an unobserved blended target continues (Alhussein & Smith, 2021; Enachescu et al., 2021). There is recent evidence that launching an intermediate reach to multiple targets typically involves longer reaction times than reaches to single targets, a result which may not be predicted if a single flexible plan is in use (Enachescu et al., 2021). The idea of a single flexible motor plan is more easily placeable within optimal feedback control theory, while the scheme wherein there are multiple competing movement plans may more easily fit into the Dynamic Systems framework.

The remaining question is how evidence accumulation processes may influence the trajectories of reaches to those targets. The traditional view, that the decision must be completed before action initiation, does not conform to the evidence that multiple motor plans can interact and interfere in various ways. If two (or more) targets are visible, then they will each have an associated action plan. The decision between those actions plans may be contingent on an evidence accumulation process, and the following section reviews some attempts to link evidence accumulation to response dynamics.

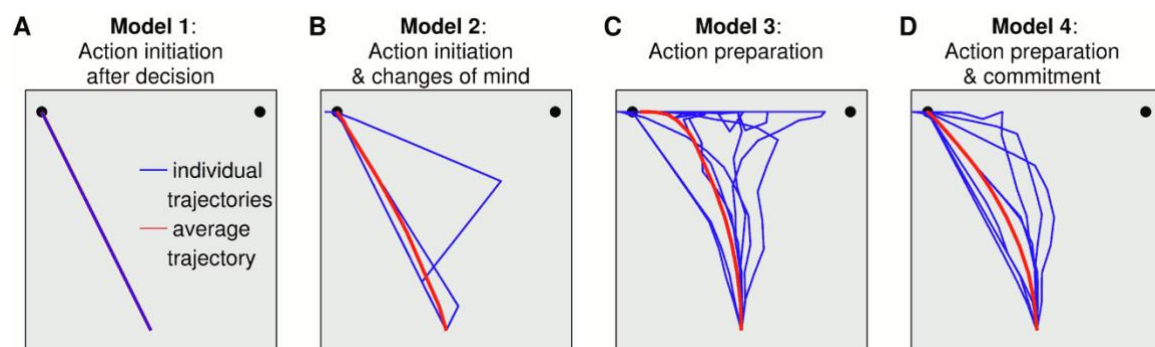
#### *1.4 Linking accumulator models to response dynamics*

There are multiple ways that the interaction of an accumulating decision with a response trajectory of an end-effector may be modelled. In a paper which compared four models of trajectory formation Lepora and Pezzulo (2015), simulated mouse movements which approximate the generation of direct movements and “discrete” changes of mind, as well as the “continuous” changes of mind often seen in mouse tracking studies. The models differ in their assumptions about the way an evidence accumulation (a standard diffusion model) links with the ongoing formation of the movement trajectory. The simplest model initiates movement once accumulated evidence crosses a decision boundary (Figure 1-7a), moving the simulated mouse cursor at constant velocity in a straight path from the start position to the response

option associated with that boundary. This could not accommodate either changes of mind or online response competition and represents the traditional decide-then-act “serial” view of perception and action.

Model 2 (Figure 1-7b) is a modification of Model 1 and extends the accumulation model to accommodate changes of mind. When either boundary is crossed, movement is initiated towards the corresponding response option, but the decision variable continues to accumulate information. If another boundary is crossed before movement to the response option is complete, there is a “change of mind” and the mouse cursor changes direction. The sharp deviations of this model were considered by Lepora and Pezzulo as “unrealistic”. Note that in this model, stimulus information was allowed to continue to flow into the movement system even after movement initiation had begun.

Figure 1-7 Four potential models to link decision-making to mouse path trajectories



Trajectories generated by the four models in Lepora and Pezzulo (2015). The blue lines are individual simulated trajectories, and the red lines are the mean trajectories. Lepora NF, Pezzulo G (2015) Embodied Choice: How Action Influences Perceptual Decision-making. PLoS Comput Biol 11(4): e1004110. CC BY 4.0

A more complex version of this idea was investigated by Resulaj (2009). Instead of responding with a mouse on desk with the cursor on a vertical display, participants grasped a vertical handle attached to a robot arm positioned underneath a horizontal screen. The workspace, RDK stimulus and response regions (to indicate overall left- or right-ward movement), and a blue circle to inform the participant of their hand location were projected onto the screen, so that

they all occupied the same plane. Unlike mouse tracking studies, the RDK stimulus vanished upon movement initiation, which allowed the researchers to investigate whether changes of mind were due to internal stimulus processing continuing during the period usually identified as non-decision time. A minority of trials from all participants showed this behaviour; the opportunity to revise the decision increased overall accuracy and incorrect initial movements tended to be preceded by moments in which that trial's RDK average motion favoured the incorrect decision. Fitting a version of an evidence accumulation model to the data, the researchers concluded that changes of mind happened because evaluation of the RDK did not stop when a response boundary was crossed. Late arriving information received during the delay between an initial boundary crossing and movement initiation could push the decision variable to rise to a secondary boundary. However, it is important to note that Resulaj's (2009) model did not generate movement paths, but the model was fit to the initiation times for all trials along with the frequency of changes of mind for each participant. In comparison to the kinds of mouse movement studies above, any kind of graded response in the movement data may have been blocked as stimulus evaluation was not able to continue during the reach, though each trial needed to be completed within 700ms. Still, in an experiment where changes of mind are possible, the balance between speed and accuracy can be controlled differently to studies which only accept initial responses. If revision of the initial decision is relatively easy to make, then that opportunity will be taken.

A more direct link of decision processes to movement trajectories was developed by Friedman et al. (2013), and incorporated intermittent control via submovements. Three participants reached from a button on a table in front of them to left or right response boxes on a touchscreen in front of them while their fingertip was tracked. Displayed on the touch screen was an RDK stimulus with between 3% and 48% coherence and shown for just 300ms at the start of the trial. If participants did not start moving within 350ms, or failed to move continuously forwards, they were given a warning signal and the trial was discarded. Participants completed hundreds of

trials over several days, as well as a condition where button-press reaction time was recorded to identical RDK stimuli. The movements of the fingertip from the start button to the screen was decomposed into overlapping ballistic submovements. These could be recombined with a similar method to the how curved reach paths were generated by Henis and Flash (1995). As a result, every retained trial was now made up of one, two or three submovements and each submovement had its own onset time, duration, x-amplitude and y-amplitude.

Friedman et al. (2013) went on to link accumulator models to the timing and generation of one and two submovement trials via simulation. A diffusion process with a drift rate dependent on stimulus quality began at stimulus onset. At the same time a one-sided accumulator controlling movement onset, with a drift rate that does not vary with stimulus quality, also began and at threshold would trigger the first submovement. If the decision process hit a boundary before the movement initiation accumulator, the first submovement has an amplitude which reaches from the start button to the selected response option, and a direction which takes it all the way to the screen. If the movement initiation accumulator hit its boundary before the decision accumulator, the direction of the first submovement is towards a position linearly related to the state of evidence accumulation (so a movement with evidence equalling zero would be to the middle of the two response options) and the amplitude for this first submovement is sampled from a normal distribution based upon the experimental data. In this case the decision variable continues to accumulate. At about half-way through the first submovement, and if the decision process has by now reached a boundary, a second submovement towards the now decided-upon response option is superimposed onto the first submovement.

The process just described uses the partial decision data to set the angle of the first submovement trajectory, while other evidence from reaching tasks suggest that initial movements are not averages between motor plans, but strategic moves directly to the centre of the targets (Wong & Haith, 2017). A modification of the Friedman et al. (2013) model was

implemented where the first submovement went in a direction uninformed by the decision variable; if it was triggered before the decision accumulator had hit a boundary the initial reach direction was set as the intermediate trajectory, regardless of the decision variable state. To arbitrate between these two models (partial information versus uninformed), the authors compared the predicted distributions of maximum deviations (referred to in the paper as “path offsets”) with the observed distributions. The partial information model provided the better fit between the model and the data.

In the models reviewed above, curved trajectories were the result of stringing together distinct submovements, where the initial submovement may be directed at the wrong target or directed at an intermediate position between the movement target locations. Lepora and Pezzulo (2015) explored two models in which there was a *continuous* flow between the evidence accumulation process and the generation of the movement trajectory. This work linked the progression of the decision variable directly to mouse trajectories from an earlier study into the “lexicality effect” (Barca & Pezzulo, 2012); on each trial participants categorized a stimulus as a word or a non-word using a mouse-tracking set up. The word stimuli were either high frequency words or low frequency words, and the non-words were either pseudowords (orthographically similar to real words) or unpronounceable strings of consonants or vowels, all of which were short enough to be read with a single fixation. The lexicality effect refers to the increase in response time for low-frequency words in comparison to high frequency words which are more readily available in the lexicon. Barca and Pezzulo anticipated that a dynamic model of decision-making and action would lead to more competition between response options, and thus more curvature in mouse trajectories when the stimuli were either low-frequency words or pseudowords.

Aiming to recreate the curved trajectories, the third model in *Figure 1-7* includes the possibility of “action preparation” (Pezzulo & Ognibene, 2012) wherein multiple candidate motor plans are available. Movement is initiated when the accumulation process begins and moves the mouse

cursor towards a position colinear with the response options, biased towards either response option by an amount corresponding with the distance of the decision variable to the decision boundaries. As can be seen in Figure 1-7c, some trajectories hit the axis connecting the two targets and fluctuate until the decision eventually resolves. This behaviour is clearly unrealistic and not observed in mouse-tracking studies. Therefore, Lepora and Pezzulo (2015) adapted this model by adding what they call a “commitment effect”. The commitment effect attracts the simulated mouse cursor to the closest response option through a bias on the decision variable itself, a form of feedback from the motor system to the decision mechanism (more on this in Chapter 4). Due to this feedback component, the authors referred to this model as a fully “embodied” model because the effector position itself is influencing the decision process. This model predicts movement trajectories such as those shown in Figure 1-4d. These trajectories certainly look more realistic, and the authors claimed that they replicated the curved mouse trajectories reported by Barca and Pezzulo (2012).

In summary, when attempting to explicitly tie evidence accumulation models to response dynamics, Resulaj et al. (2009) succeeded in linking the initiation times and response proportions, both initial and final, to an evidence accumulation process but not the movement trajectories themselves. Though it must be noted that Resulaj’s experimental set up did not allow for intermediate movements. Building on the change of mind model, Lepora and Pezzulo (2015) simulated trajectories where a reach was triggered with constant velocity but few other biomechanical considerations, resulting in “unrealistic” trajectories composed only of straight line movements, all towards the response options. Deciding that constant online control was more plausible, and building on the ideas of parallel motor planning, they implemented further models which started the movement coincidental with the start of evidence accumulation, with the direction at every timestep fully determined by the state of the decision variable. To coerce this model into generate smoothly curving trajectories, a “commitment effect” was added to represent the inclusion of embodied information. In contrast, Friedman et al. (2013) included a

variety of assumptions about the generation of movement trajectories, including intermittent control and the availability of “partial” information about the stimulus only at certain times during the execution of submovements. Comparing this model to one that only allowed pure intermediate movements (without any stimulus information), they concluded that stimulus information must be accessible to the motor system when launching reach movements.

### *1.5 Conclusion*

To summarise, the application of mathematical models to human decision-making performance has revealed much about the basic processes underlying this fundamental feature of human activity (Ratcliff et al., 2016). The most successful of these are evidence accumulation to bound models in which activity (noisily) ramps up to a threshold, after which a response is selected. These models can be used to parsimoniously explain behavioural data such as reaction time and accuracy in button press tasks to perceptual stimuli and have often been extended to explain higher-level cognitive processes (Evans & Wagenmakers, 2020).

At the same time, there is mounting neural evidence which suggests that motor areas of the brain may often be the location for this evidence accumulation, particularly when the response to the decision involves movement, such as a saccade of the eyes or a reach to a location (O’Connell & Kelly, 2021). Given this link, there is now a large body of research, principally using mouse tracking, which depends on the assumption that the decision and response selection processes are occurring somewhat in parallel and are closely integrated, if not one and the same (Schulte-Mecklenbeck et al., 2019). Mouse tracking has become nearly ubiquitous in a wide variety of psychological research into higher-level cognitive processes (Freeman, 2018). While it has been noted that many degrees of freedom in terms of study design and analysis can have a large influence on the results (Kieslich et al., 2020), the idea that reach trajectories (as recorded



via mouse cursor) reflect the status of an ongoing decision process is a core assumption underlying much of the research.

Responding with a mouse cursor, however, is not the same thing as the kinds of natural movements that human beings, or any animal, evolved to interact with their environment.

Reaches with the whole arm, rather than slight manipulations of a computer mouse, may allow a larger window into the decision process (Gallivan & Chapman, 2014). Moreover, a naturalistic reach-to-grasp action may permit more insight into the interaction, or co-action, of perceptual and motor decision processes.

As well as potentially providing more insight into how decision processes and motor processes are intertwined, this work may also provide a valuable starting point for detecting uncertainty in ongoing goal-directed actions. If, for example, decisional uncertainty may be inferred from movement, that opens the door to applications which monitor movements and can provide assistance at points of high uncertainty (Bleser et al., 2015).

## *1.6 Thesis Outline*

This thesis will use the measurement of three-dimensional reaching movements, to investigate how perceptual uncertainty about the target may influence reach-to-grasp trajectories. In this more ecologically valid scenario than work using RDK stimuli or delayed target cueing, will the “attractive” effects of a non-selected target show up in a reach-to-grasp action? If there are such attractions, can these be linked to an embodied model of choice reaching trajectories?

Chapter 2 will present two experiments in which participants had to decide between and then reach and retrieve one of two real objects placed in front of them within a time limit. Two main aspects of the task were manipulated. In both experiments there were two levels of perceptual difficulty, and in the second experiment participants were put under time pressure to initiate movement. Increasing perceptual difficulty increased deviation towards the non-target, as did

imposing the movement deadline, indicating that the deadline increased the proportion of reach trajectories that started with less information. It was observed that beyond the decision processes, there are major sources of variability and bias from biomechanical constraints on the reach paths, as well as variability in the motor response.

Chapter 3 will present another experiment where early reach initiations were encouraged by a deadline. To help account for biomechanical constraints, many more trials were recorded from each participant, including baseline trials where no decision process was required. Aggregate analyses between easy-choice trials and hard-choice trials replicated the results from Chapter 2. Distributional analyses were also conducted to see if the pattern of path deviations like those seen in Chapter 2 were attributable to either modifications to the shape of the no-choice curvature distributions, or whether these were better explained by a combination of distributions. The analysis showed that drawing reach curvatures from a combination of the baseline distribution and an additional distribution described choice reaching better than the alternative. From this it was concluded that any model that links decision accumulation to reach trajectories must be able to account for both the baseline variability and the influence of choice processes.

Chapter 4 will present a simulation study which systematically explored the fully “embodied choice” model from Lepora and Pezzulo (2015) as a starting point for simulating choice reach trajectories. The model approximates the decision process with a random walk in discrete time, with free parameters for the mean drift rate and decision noise. Decision information continuously flows to the reach generation algorithm which calculates the distance between the decision variable and the decision boundary to set the current heading of the simulated effector. This modelling used the baseline trajectories from Chapter 3 to see whether a combination of those and the curvatures generated by the embodied choice model could resemble the empirical distribution of hard-choice reach curvatures. The model was further developed to

simulate a change-of-mind process were each random walk started at the decision boundary.

Neither model fully captured the characteristics of the data generated experimentally.

Chapter 5 is a general discussion of the work presented alongside a set of possible future directions for this work.

## Chapter 2      Increased perceptual uncertainty during timed reach-to-grasp actions increases path deviation

Chapter 2 details the development of an experimental paradigm that could elicit curved reach trajectories and potentially other kinematic hallmarks of an evolving decision variable in a reach-to-grasp action.

Experiments 1 and 2 were designed to elicit two forms of motor behaviour that may show increased variance under conditions of increased uncertainty: reach path deviation and wrist orientation. Perceptual uncertainty was manipulated by having two “difficulty” conditions with pairs of objects that had either dissimilar luminance (the easy condition) and more similar luminance (the hard condition). These objects were graspable, within reach, and oriented to require two different wrist rotations to pick up. The experiment used a liquid crystal screen to occlude the objects from the view of the participants until each trial started, at which point the participant had to identify, select, reach for and retrieve one of the two objects according to the experimenter’s instruction and within an overall time limit per trial.

The data from these experiments were processed to extract the reach initiation time, the movement time and the overall reach time, as well as the deviation of the reach path from an ideal trajectory; summarised as the area between the recorded path of the first knuckle on the right hand and the straight line from the start position to the final position of the knuckle marker, as well as the orientation of the hand during the execution of the reach.

Mean differences in overall time, initiation time, movement time and mean curvature were found when reaching and grasping under increased perceptual uncertainty. Some of these effects remained when “change of mind” trials, defined as reaches which initially curved towards the non-target, were removed. Statistical analyses of the results from both experiments were conducted by constructing linear mixed effects models (LMM) of the data. Experiment 2

implemented a time pressure on movement initiation, using feedback to the participant if a reach was not initiated within 400ms after the start of a trial. Mean differences in both timing and curvature measurements remained after removing change of mind trials from the results of either experiment.

## *2.1 Background and rationale*

As reviewed in Chapter 1, psychological research which uses mouse tracking data to study the dynamics of cognitive processing is closely linked to the assumptions of the embodied cognition research program (Freeman, 2018; Garbarini & Adenzato, 2004). These assumptions are supported by research into decision-making which has identified correlations between neural activity in motor areas of the brain and computational models of evidence accumulation and suggests that when making a choice, we are choosing between potential motor plans (Cisek, 2007, 2012). Early research into the generation of curved trajectories made by participants holding a stylus onto a digitizer table established that a competing target in the environment may cause curvature away from the distractor if there is time for active inhibition (Tipper et al., 1997), or show curvature towards an original target location, if a target switch occurred soon enough after a trial started (Flash & Henis, 1991). Thus, the curvature of trajectories recorded in mouse tracking research may be seen as a hallmark of the competition between motor plans. However there is still debate over whether the curved trajectories elicited in these studies require multiple motor plans to be simultaneously active (Dekleva et al., 2018; Nashed et al., 2014) and whether it is the visual representations of targets or their associated motor plans which are decided between (Enachescu et al., 2021).

One side of the debate claims that multiple movements are generated in parallel, and then decided between as a competitive process (Cisek, 2007). Actions triggered before this decision is finished will show mixed trajectories as the movement plans interfere with each other (Chapman et al., 2010). The other side claims that to achieve the desired speed and accuracy

only one initial single trajectory will be planned and executed (Wong et al., 2015). This direction of the initial trajectory will then be to a location in between the actual target locations, allowing the agent to hedge their bets over which target will be eventually selected and will, once sufficient evidence has been accumulated, divert their reach path to the selected target (Haith et al., 2015). In most of these studies two potential reach targets were presented to participants with the real target cued only once movement begins, referred to as “go-before-you-know” studies, which can be contrasted with “go after you know studies” when a target cue is available before movement (Gallivan et al., 2018). Neither of these approaches, however, require any accumulation of evidence – a potential reach target is either cued or not. Thus, it remains to be seen whether the dynamics of perceptual decision-making, driven by rates of evidence accumulation, response thresholds, urgency signals, and motor strategies will have an influence on the kinematics of the response, be that in the initiation time of the movement, the duration of the movement or the curvature of the path.

It must be kept in mind that most of the reaching studies which investigated the effects of target displacement (i.e., Flash & Henis, 1991) examined the performance of participants as they moved a stylus over a table. Mouse-tracking studies inevitably confine their participants to respond by pushing an electronic device across a tabletop. The handful of studies that recorded three-dimensional reach trajectories required only a motion to bring the tip of the index finger to target locations on a touchscreen (Chapman et al., 2010; Friedman et al., 2013; Wong & Haith, 2017). However, reaching is nearly always much more interactive. Pointing is a nearly exclusively human behaviour, used to direct another’s attention towards something of interest (Miklósi & Soproni, 2006). In contrast, the multi-step action of reaching out, grasping an object and then moving it to another location is seen in many animals (Karl & Whishaw, 2013), so it may be regarded as a highly ecological from an evolutionary point of view.

### 2.1.1 Reaching to grasp movements

Jeannerod (1988) suggested that reach-to-grasp movements are composed of two independent but concurrent movements, with the reach requiring extrinsic information about the object, such as location and orientation, and the other requiring intrinsic information about the object, such as size and shape. Coordinated by visual control, the transport phase moves the hand to the location of the reach target, and the manipulation phase shapes the fingers for the grasp. The independence of reaching and grasping is supported fMRI studies which differentiate the object identity path in the ventral stream from a dorsomedial object location stream and a dorsolateral grasp stream (Fabbri et al., 2014; Valyear et al., 2006). Ventral areas of the cortex, which code object identity, become more involved as the complexity of a required grasp increases (van Polanen & Davare, 2015).

During natural behaviour, of course, reaching and grasping are tightly coordinated (Rouse et al., 2018), and the neural implementation of this coordination must happen somewhere in the motor or premotor cortices. If the same grip shape is required on an object, even if rotated in space, there is little variation of the transport kinematics which those reach and grasp action have in common and increased variation for the wrist joint (Lacquaniti & Soechting, 1982). However, when a reach is succeeded by a precision grip rather than a power grip, the increased accuracy required to successfully place the fingers onto the object will influence transport kinematics, slowing down the latter phase to aid accurate finger placement (Gentilucci et al., 1991). It's not just that the grasp points that need to be hit precisely – the angles that the fingers need to approach the surface of the object should be perpendicular to the surface, too. When picking an object off a table, the fingertips widen, approaching the grasp points from above before curling onto the object sides (Verheij et al., 2012, 2013). The object's size, shape and orientation determine where the fingers need to be to start the grasp action, so the destination for the transport component will be determined by intrinsic properties of the target, as well.

### 2.1.2 Online control of reach-to-grasp

The effect of grasp object location on reach-to-grasp paths was studied by Paulignan et al. (1991). In the experiment participants were to reach, grasp, and lift one of three dowels which were visible before the trial started. In this experiment online corrections to the reach trajectory were observed within 100ms of a target switch. In another study the fingertip kinematics of participants were observed as they reached out to grasp a wooden cube which could be gripped across multiple axes (Voudouris et al., 2013). In some trials the cube rotated, and a change in finger trajectory was seen within 160ms of the perturbation. Interestingly, many subjects altered their flight to use the originally selected grasp points even when the rotation presented new grasp points which would have been easier to reach. This highlights how an intended manipulation can have a persistent influence on the transport component of a reach-to-grasp action.

Comparing the effects of visual feedback on pointing movements and grasping movements, Carnahan et al. (1993) found that the early part of a pointing movement (i.e. before peak velocity was reached) was often unaffected by a change in target location. However, when grasping for location-perturbed objects, velocity peaked later in the reach. Additionally perturbed grasp trajectories had lower peak velocities, relative to un-perturbed grasp trajectories, indicating earlier opportunities for intervention after visual feedback about the action objective.

The reach-to-grasp action, then, given its deeper evolutionary origins and the multiple interacting pathways which travel from the visual cortex to the motor cortex, may be less “ballistic” than simple pointing movements. When pointing there is no actual interaction with the object that’s the target of the “reach”, and the action of a mouse click seems similarly superficial. Therefore, it remains to be seen whether the decision-related effects seen in mouse movements generalise to full 3D reach-to-grasp movements.



Given the costliness of making an action with the hand, and the higher fingertip precision required for successful grasping, it is conceivable that reach-to-grasp actions will follow the classic “decide, then act” model of decision completion before initiation (Gold & Shadlen, 2007). Reach-to-grasp paths will then default to a serial process just with the a possibility of occasional changes of mind (Resulaj et al., 2009). Alternatively, if as suggested by embodied cognitivists there is continuous flow between decision mechanism and movement generation (cf. Lepora & Pezzulo, 2015), we would expect to see the trajectory mixing that is often reported in that literature: movements may initially be aimed in between the two objects before they bend around to the target. On the other hand, the control of reaching movements may only be intermittent, and the initial intermediate aim point may come about because of concurrent activation of two motor programmes when the reach is triggered, balanced according to the state of the decision process at initiation (i.e. target blending; Friedman et al., 2013; Gallivan et al., 2015). A final possibility is that participants may have no access to a decision processes that has not yet hit threshold, and instead aim in between the objects with a view to correcting their movement once the decision process has run its course (Wong & Haith, 2017).

### 2.1.3 Overarching question

The overarching question of the experiments presented in this chapter is to ask how target uncertainty, induced *via* perceptual uncertainty, will influence reach-to-grasp actions. Will the constraint of picking up a target default behaviour back into a classical decide-then-grasp scheme? Or will the slower and more highly controlled reach-to-grasp action show hallmarks of continuous control? A schematic of the models and how they suggest reach-to-grasp trajectories will be affected can be seen in Figure 2-1.

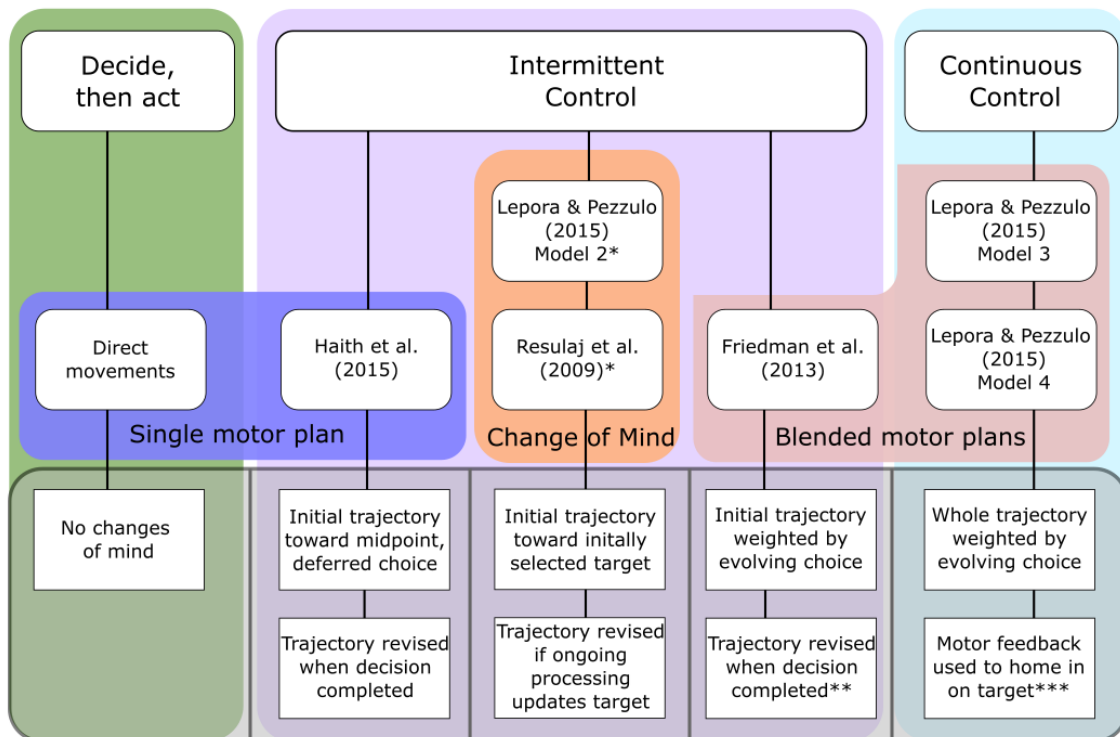
There are three potentials high level mechanisms for how decisions and reach paths are related. The “decide, then act” mechanism reflects the serial model where all decisions are completed before any motor programming or initiation can occur. The second high level mechanism is that

of intermittent control where the state of the decision variable can occasionally influence the reach path. The final mechanism is that of continuous control, where the decision variable and the reach path are continuously connected.

For the “decide, then act” mechanism, a single motor plan to achieve that end is generated and then executed, but only once a decision is fully resolved. Within the intermittent control class of mechanisms there may be either a single motor plans active at any one time, or multiple motor plans. If a single motor plan is only available at reach initiation, then that plan may be informed or uninformed about the state of the decision variable. For Haith et al. (2015) the motor plan is uninformed by information gathered on the current trial and will be towards a location biased by target location probability, and in the case of equal target probability be aimed directly forwards. Once a decision process resolves, a new motor plan is generated and executed to transport the hand to the target location. This model can be contrasted with Friedman et al. (2013), where the initial action *is* informed by current evidence, and the blending of that evidence influences the initial reach direction. Sitting between these (on the schematic) is the “change of mind” model. This mechanism does have access to currently accumulating information, but only as a categorical output as it executes a motor plan free from interference from the unfavoured option; further control will be exerted if the decision process settles on a different target before the reach action is completed. Finally, the continuous control mechanism represents a high-fidelity coupling between evidence accumulation and the reach action. In this scheme the evolving decision variable regulates the activity of parallel motor plans, and their combined, weighted influence is directly observable in the reach path.

Figure 2-1 Schematic of models and their hallmarks of those effects in reach-to-grasp

trajectories



Note. The “Decide, then act” scheme is if task demands push the participants to default to a “serial” processing strategy.

\*Model 2 from Lepora and Pezzulo (2015) and the model from Resulaj et al. (2009) does not make sophisticated claims for the shape of trajectories, and they are included under “Intermittent Control” as control must be applied at some point to implement a “change of mind” on the trajectory.

\*\*The Friedman et al. (2013) model suggests that control occurs due to overlapping submovements, and a revision will only be necessary if the first submovement was triggered without complete information.

\*\*\*Motor feedback was applied to Model 4 from Lepora & Pezzulo (2015) only and represents feedback from the motor system into the evolving decision.

The studies presented below develop a paradigm which can explore all these options. Much as in real life, the decision which needs to be made will be a choice of one of two objects according to an intrinsic property (in this case – luminance), and this choice will have two difficulty levels. The objects will be arranged symmetrically so that different movements are required to execute the reach and grasp, but with similar movement extent and eccentricity from the midline. As a further manipulation, the grasp objects will be rotated so that the grasp points will be

horizontally oriented or vertically oriented, and the alternative target will have a congruent, or incongruent orientation.

#### 2.1.4 Specific Hypotheses

The hypotheses for these studies are set up to separate out the effects of decision uncertainty and other constraints on the reach and grasp movement. Reach paths, reach timing, and grasp dynamics will depend on participant individual differences, workspace effects of target orientation and position, and the difficulty of the perceptual task. Each reach path will be summarised by AUC, defined as the area captured between the actual path to the target and the ideal direct path from the start position, once projected onto the horizontal plane (see Figure 1-2). It is expected that each participant will have their own distribution of initial response time and movement time to each target side and target orientation, as well as a baseline curvature.

So, when controlling for each participant's biomechanical constraints, the prediction is that as perceptual choice difficulty increases so will the overall latency between target presentation and target grasping. The longer duration between stimulus presentation and grasp will be mediated by either delayed action initiation, a longer movement duration, or both. Additionally it is expected that increasing perceptual choice difficulty will introduce more curvature into the distribution of reach paths as either: (i) an increase of the incidence of changes of mind, (ii) an uninformed initial reach trajectory which for difficult trials will be updated later in the action, (iii) an initial trajectory informed by relative evidence at launch, but only modified intermittently, or (iv) a continuous reflection of an evolving decision which is gradually resolved as the reach progresses. Furthermore, to assess whether it is only "changes of mind" that lead to increased reach time and curvature, analyses will be rerun with "change of mind" trajectories removed. Should any effects of perceptual uncertainty survive this filtering, then its influence goes beyond simply sending participants in the wrong direction occasionally.

The uncertainty introduced by increasing the difficulty of the perceptual task may be more evident when participants need to initiate their reaches very soon after the trial begins. To encourage early movement, and perhaps increase the “uncertainty” of reach-to-grasp actions, the second experiment implements a feedback mechanism to inform participants whether or not they successfully initiated their reach within a pre-set time limit. Response deadline manipulations on perceptual decision-making tasks typically reduce boundary separation, thereby encouraging speed over accuracy. If reach-to-grasp responses follow a “decide, then act” or pure “change of mind” pattern, then there will be a greater proportion of incorrect reaches, or changes of mind trajectories. Alternatively, a time limit may bring the experimental paradigm closer to a “go-before-you-know” type study and thus increase intermediate trajectories via either motor plan blending or the use of strategic “decision deferral” motor plans.

## 2.2 *Methods*

### 2.2.1 Participants

Participants attended a single ~1hour session for which they received course credit or a fee. Across both experiments 62 participants were tested; 32 in experiment 1, and 30 in experiment two. Investigations into rapid reaching with target uncertainty typically use fewer participants than this with Ns of between 10-20 being typical in each experiment (Chapman et al., 2010; Dekleva et al., 2018; Enachescu et al., 2021; Gallivan et al., 2015; Gallivan & Chapman, 2014; Wong & Haith, 2017). However, it is well known that studies in psychology are often under-powered, so I aimed for a sample twice the size of that used in many previous studies. Right-handed participants were recruited from the local population or from the undergraduate cohort. No participants were excluded from experiment 1; one participant from experiment 2 was excluded due to equipment malfunction (final N=29). Ethical clearance was obtained from the

local Faculty of Science Human Research Ethics Committee. All participants provided written informed consent and were fully debriefed.

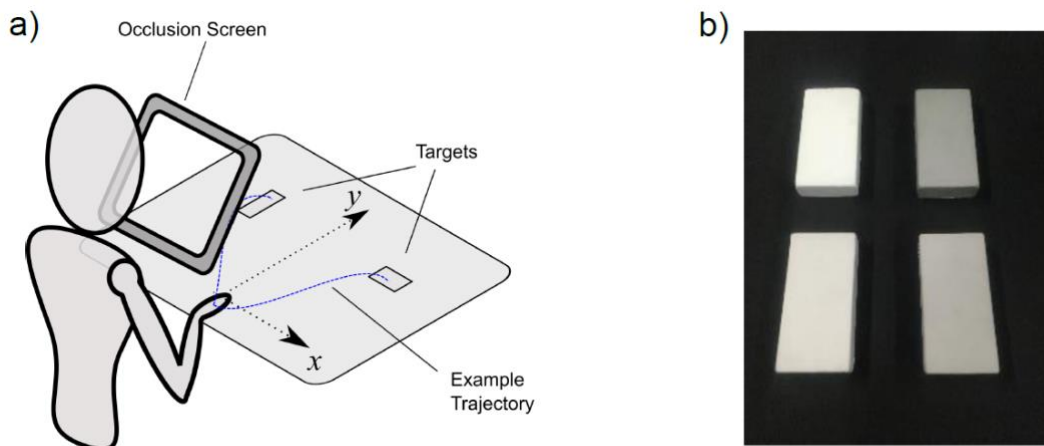
### 2.2.2 Design

We adopted a fully repeated measures design. For each participant, we recorded 96 trials, organised into six experimental blocks of sixteen trials. Four experimental independent variables were manipulated: Difficulty (Easy vs Hard), Target Side (Left vs Right), Target Orientation (Vertical vs Horizontal) and Distractor Orientation (Congruent vs Incongruent). These four factors were combined to form 16 unique trials presented in a randomised order within each experimental block. For three experimental blocks the participant was to pick up the brighter target, and for the other three the darker target. Bright and dark instructions alternated between experimental blocks.

### 2.2.3 Materials

Participants were seated on an adjustable chair at a table of 80cm height. The motion of their hand was measured using a 12-camera Qualysis (AB) System (Oqus 300 cameras), sampling the marker positions at 100Hz. The capture space is measured in millimetres and calibrated so that the starting position of the hand is at the (0,0,0) point, the y-axis of the space increases directly forward of the participant, the x-axis of the space increases from left to right, and the z-axis of the space increases upwards. See Figure 2-2 for a diagram of the experimental setup (a) and a photograph of the experimental stimuli (b).

Figure 2-2 Experiment Set Up and Stimuli



*Note. a) Experiment setup schematic and b) the two pairs of stimuli used for easy decision trials (top) and hard decision trials (bottom).*

The table was covered with a black cloth, upon which the starting position was marked with a cross of white tape, with two further crosses to mark the centre of the stimulus positions. Each of these were 20cm forward of the starting position and 30cm apart from each other. Thus, the centre of each target was 25cm from the starting position. For Experiment 2 a sprung switch, covered by a metal plate, was fixed to the table at the starting position and also covered with the black cloth. When participants rested their hand at the starting position a small amount of pressure was needed to push the button down. This was to record launch times and provide feedback to the participants on their launch times. Subsequent analysis showed that the difference between the estimated movement onset time and the button release time was highly variable, so button release times were not used in any analysis step.

To obscure the targets until the trial began, an A4 sized liquid crystal film ([www.prodisplay.com](http://www.prodisplay.com)) between two panes of clear glass was mounted between the participants' line of sight and the stimuli. The transmittance of light through the film is 88% when a current is applied and 60% when it is not, and the haze coefficient is 3% when switched on and 98% when switched off. The switch from opaque to clear (and vice versa) was controlled by a laptop (TOSHIBA TECRA R950), running custom code in MATLAB 2017b (MathWorks Inc.). This programme also communicated

with the motion capture system over a direct ethernet connection to set event markers on the motion recordings and generated a random trial order for each participant.

A total of five passive infrared markers were fixed to the wrist and hand of each participant. One on each of the thumb and index fingernails, one over the knuckle of the index finger, specifically the metacarpophalangeal joint, one on the ulnar styloid (the lump of bone near the outside edge of the wrist) and finally over the radial bone parallel to the ulnar styloid. The markers on the fingertips were to be used to track finger aperture, the knuckle marker was used to track overall hand position, and the wrist markers were intended to be used to track the orientation of the wrist at grasp.

The stimuli were a set of four cuboid blocks of dimension 10x5x2cm (l x w x h) and each was painted with matte grey Dulux paint, with light reflectance values (LRV) of 72, 62, 45, and 31, corresponding under laboratory lighting conditions to luminance values of 56.7 cd/m<sup>2</sup>, 41.1 cd/m<sup>2</sup>, 30.0 cd/m<sup>2</sup>, and 22.3 cd/m<sup>2</sup>, respectively. The stimuli were presented as a high-contrast pair (56.7 cd/m<sup>2</sup> vs 22.3 cd/m<sup>2</sup>) for the easy choice trials and a low contrast pair for the hard choice trials (42.3 cd/m<sup>2</sup> and 30.0 cd/m<sup>2</sup>). A fifth block with a LRV of 53 and measured luminance 42.3 cd/m<sup>2</sup> was used as a practice target to familiarise the participants with the experimental procedure and the required reach direction, extension, and grasp.

#### 2.2.4 Procedure

Participants were asked to attend the session wearing a loose top to allow full motion of the arm. After they were given information about the experiment and provided informed consent, the markers were attached to the hand and the height of the chair was adjusted so that (i) the stimulus positions were visible through the screen, (ii) participants had an unobstructed view of their hand in the starting position, and (iii) participants could reach both target positions freely.



The experiment consisted of four practice trials (each with the 52% LRV block in either the left and right positions and at a horizontal or vertical orientation) and 96 experimental trials. Before each trial the experimenter arranged the blocks on the table according to a pseudo-randomised order generated by the MATLAB script, the participant was reminded to reach for either the brighter or darker block, and finally the experimenter triggered the trial sequence. Each trial began when the screen turned clear, with no other warning or preparation tones. At the same time the laptop controlling the LCD screen also sent a message containing trial condition information to the motion capture recording system.

For experiment two, the time that the desk-mounted button was released was recorded. The time between the screen opening and the button release was also sent to the motion capture software, and if this time delay was greater than 400ms an aversive buzzer was sounded. It was discovered during data processing that there was a large variability between the time that the button recorded hand lift-off and the time that the knuckle marker exceeded the velocity threshold for movement initiation (see subsection 2.2.5.3 for the threshold), so these values were not used for further analysis.

## 2.2.5 Data Processing

### 2.2.5.1 Analysis Pipeline – Raw Motion Capture Data

Data from each experimental block was saved into a separate file by the motion capture system. Automatic identification of markers was used to label the trajectory data, and these trajectories were manually inspected to check that marker position was accurate, and to fill any gaps in the trajectory information. The capture space was recalibrated at least once every 5 experimental sessions, with the origin of the space in the same location as the starting position.

Automatic identification models were used within Qualisys to identify each of the five markers, each motion capture file was manually checked to ensure consistent marker identification in the

case of gaps in the recording. Automatic gap filling was applied using the default settings for Qualisys QTM.

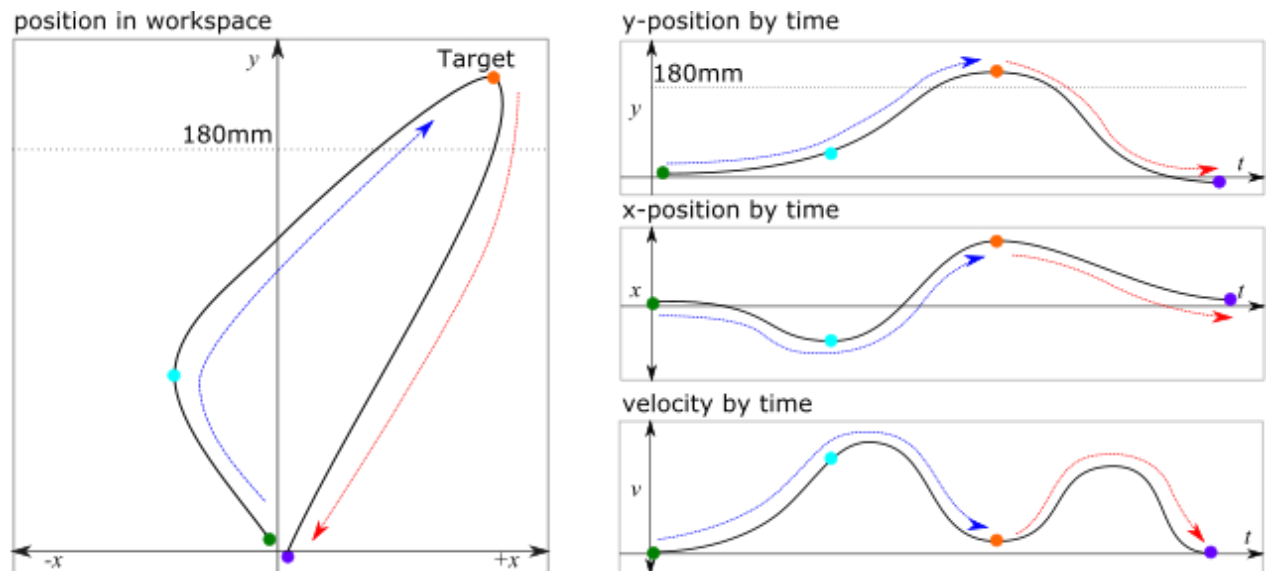
#### *2.2.5.2 Analysis Pipeline – Exported Data*

The identified trajectory information was exported to MATLAB for further data processing and analysis. Each file consisted of one experimental block, out of six in total, lasting approximately 10 minutes and contained the position of each marker at each 100<sup>th</sup> of a second, along with the trial information and trial start times. The data from each marker was passed through a bidirectional low-pass Butterworth filter with a cut-off frequency of 10Hz and order 4, which smoothed the signal without introducing phase distortion. The 10Hz cut-off is standard in movement research and used to smooth out measurement noise in reach tracking studies (Gallivan & Chapman, 2014; Ulbrich & Gail, 2021), though some studies have used a 20Hz cut off (De Comite et al., 2021; Friedman & Korman, 2012). The removal of high-frequency noise from the trajectory information is important for this study to allow the extraction of reliable features, such as peak velocities and direction reversals, which are used to identify the beginning and end of the reach moments. A comparison of the filtered and raw trajectory data is presented in Appendix A.

The time that the event marker was received by the Qualisys system was used to identify the first of 300 frames of motion capture data to be used to analyse each trial, to allow for trajectory landmarks such as the motion end to be identified. As can be seen in Figure 2-2 and Figure 2-4, the x-axis was the left-right direction and the y-axis the forward-backward direction, both relative to the participant and workspace with the z-axis unlabelled in the diagram, but recorded as the up-down direction. The y-axis ( $x=0$ ) was on the midline of the participant. Subsequent processing and analysis only used the x and y coordinates. Next, the 'findpeaks' function was applied to the y-axis data for the knuckle marker trajectory and a peak of over 180mm was used to initially estimate the trajectory part where the hand reversed direction to retrieve the block.

The recording frame closest to the y-axis reversal at which vectorial velocity was slowest was used to define the end of the reach motion (see Figure 2-3).

Figure 2-3 Schematic of A Reach and Retrieve Action

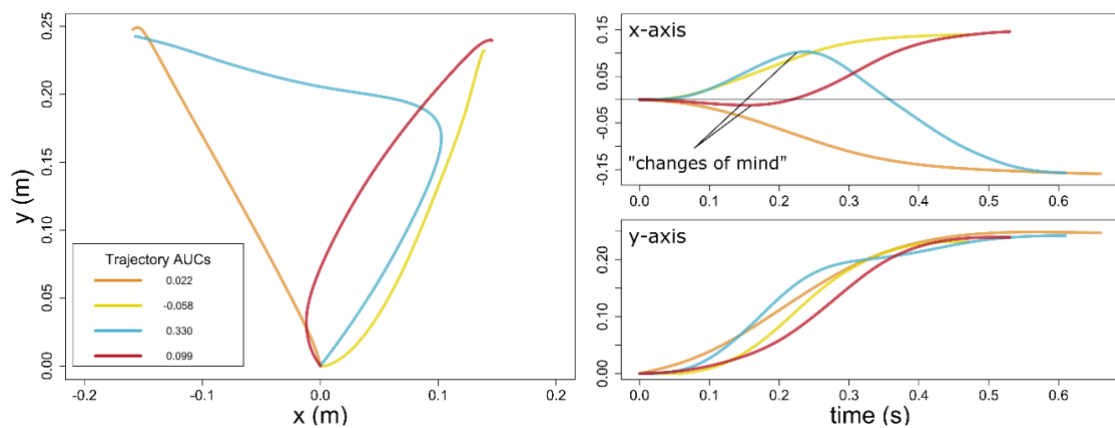


*Note.* Left panel shows one reach, grasp and retrieve action. the right top panel shows the y-positions with respect to time, and the right middle panel shows the x-position with respect to time, and the right lower panel shows the velocity. Annotations: The green dot is the starting position, the blue arrow shows the reach towards the target, the teal dot shows a change of direction in the x-axis, the orange dot shows the endpoint of the reach phase, the red arrow shows the retrieve phase of the action, and the purple dot shows the end of the retrieve phase. The dashed line at  $y=180\text{mm}$  can be seen in the left panel and the right top panel, to demonstrate how the reach phase of the action was identified.

The ‘findpeaks’ function was also used to detect whether the reach trajectory was a correct, incorrect or a “change of mind” reach using the x-axis data for each trial. With the x-trajectory flipped so that positive peaks indicated a movement towards the correct target, a trial at which there was only one peak at the end of the movement defined a correct reach (such as the yellow trajectory in Figure 2-4). Trials with only negative peaks defined an incorrect reach (such as the orange trajectory in Figure 2-4). A change of mind trial was identified if there was a peak or trough in the x-axis measurement, and this change was located on the opposite side to the final pick-up (see Figure 2-3). Defining changes of mind in this way guarantees that there is at least some observed movement towards the alternative grasp object. Analyses presented later in this chapter will test for effects of difficulty with these trials removed from the data set. This is

because some theoretical explanations predict movements to only one object or the other (and not in-between), when stimulus information is available from the trial start contrary to the go-before-you-know type studies (see Gallivan et al., 2018, for a review). This definition is also analogous to “x-flips” in the mouse-tracking literature (Freeman, 2018).

Figure 2-4 Four Sample Trajectories



*Note.* Left panel shows four trajectories plotted in x and y coordinates, each starting at (0,0). The right panels show the x and y positions against time. The orange path shows a reach which proceeds directly to the left target, the yellow trajectory shows a reach which pulls away from the ideal line to the right target, and the blue and red trajectories both show “change of mind” trials with a late change (blue) and an early change (red). All change of mind trials were identified by examination of the x vs time plot of the reaches.

To remove variance arising from slightly different starting hand positions in each trial the smoothed trajectory was translated to start at 0,0,0, by subtracting the difference between the origin and the position of the knuckle marker at trial start.

### 2.2.5.3 Analysis Pipeline – Extracting Relevant Measures

Overall time was calculated using the number of frames between the trial onset marker, and the slowest point of the reach once the knuckle marker was more than 150 mm forward of the starting position. Initiation time was calculated using the number of frames between the trial start and the frame at which the knuckle marker’s velocity exceeded 5% of the maximum velocity during the trial. Movement time was calculated as the difference between the overall time and initiation time in seconds.

To calculate the curvature measure, all samples between the movement onset and end were extracted, adjusted to start at 0,0 and normalised so that the Euclidian distance between the start point and the end point was 1. The polygonal area between the trajectory and the ideal straight trajectory was saved as AUC. Trajectories that curved towards the distractor and then back towards the target were assigned positive AUC values, while trajectories that curved away from the distractor were assigned negative AUC values (see Figure 2). Should a trajectory contain both positive and negative curvature, the overall AUC is the sum of the positive and negative components.

#### 2.2.6 Statistical Analysis

The primary analysis strategy taken with these data was to use linear mixed effect modelling (LMM). While the standard approach for repeated measures designs would be to use analysis of variance (ANOVA) techniques, LMMs allow for a more flexible approach that avoid aggregating data across trials and can tolerate different numbers of trials across conditions (e.g. as a result of trials discarded due to a motion tracking error, or an overall incorrect reach). There is no single agreed approach to implementing LMMs (Meteyard & Davies, 2020), but the usual goal is to find a parsimonious model which can be used to estimate the effect sizes of experimental manipulations and their interactions.

Data were analysed using the *lmer* package (Bates et al., 2015, 2021) in RStudio (R Core Team; RStudio Team, 2020). A saturated model, which includes all possible main effects and interactions, is specified and then the backwards elimination procedure ("step"; Kuznetsova et al., 2020) is used to iteratively identify the least useful term in the model based on improvement in AIC, and remove it. This procedure is repeated until removal of the least useful term does not lead to an improvement in AIC. There is controversy around this technique as automated procedures using arbitrary significance thresholds may bias results (Harrison et al., 2018). However, for our purposes the goal of the analysis is to test for hypothesised simple workspace

and trial difficulty effects on reach timing and curvature, while being flexible enough to spot unexpected interactions between those effects.

The variable used for analysis of initiation time, movement time and overall time is the negative inverse of the measured timing variables (e.g.  $-1/X$ ). A priori, the effect of interest for all the following analyses is that of choice difficulty on the timing and curvature of the reaches.

Alternative transformations of the timing variables were tested, however none of these altered the main conclusions of the reported analyses (see Appendix A for a summary of these analyses).

In the design of both studies reported below the orientation of the targets was manipulated so that half the targets were horizontal, and the other half were vertical. Additionally, for half the trials the distractor target had the same orientation as the target, and for the other half of the trials the distractor orientation was incongruent. The purpose of this manipulation was to explore the possible influence of ongoing decision making on grasp shaping, as this is driven by the intrinsic properties of the reach target, such as the orientation and size, rather than the extrinsic property of the location. If, for example, reach and grasp actions are specified in advance of the reach, and incongruent target orientations increase the complexity of this computation, then an interaction between difficulty and orientation congruency will arise in the initiation time for the reaches. Another possibility is that target positions requiring reaches that are more awkward to execute may simply take longer and thus allow more time to implement a corrective action within the reach. This could lead to difficulty having a greater influence on reach curvature towards targets on one side of the workspace than the other. The analysis approach taken here aims to

## 2.3 Results

### 2.3.1 Experiment 1

Out of all 3072 trials (32 participants completing 96 trials), motion tracking errors led to five trials being dropped from analysis; two from the easy condition, and three from the hard condition. Eight trials were removed because the end of the reach was not detected within two second of the trial start: one from the easy condition and seven from the hard condition.

There are four kinds of reach categorised for this experiment: (i) completely correct (where the requested target was retrieved without any change of mind), (ii) correct with change of mind (where the participant initially reached for the incorrect target, but eventually picked up the correct target, or in rare cases changed their minds twice during a reach), (iii) completely incorrect (where the requested target was not picked up and there was no detected “change of mind”), and (iv) incorrect with change of mind (where the participant initially reached for the correct target, but eventually picked up the incorrect target). The average number of completely correct trials for each participant was 77.5 (range: 61-91), the average number of correct with change of mind trials was 14.8 (range: 3-35), the average number of completely incorrect trials was 3.1 (range 1-9) and the average number of incorrect with change of mind was 1.83 (range: 1-7). 116 trials were removed because the incorrect target was picked up, six from the easy trials, and 110 from the hard trials.

Table 2-1 Count and proportion for each reach type within choice difficulty condition

Choice Condition	Correct Reaches (tot = 2950)		Incorrect Reaches (tot = 117)		Total
	Direct	CoM	Direct	CoM	
Easy	1246 (81.2%)	282 (18.4%)	6 (0.4%)	0 (0%)	1534
Hard	1039 (67.8%)	383 (25.0%)	78 (5.1%)	33 (2.2%)	1533
Total	2285 (81.0%)	665 (15.2%)	84 (2.7%)	33 (1.1%)	3067

Note. Table rows show the total count of trials in each condition, pooled across participants, and the columns divide those trials between correct reaches (where the correct target was grasped) and incorrect reaches (where the distractor target was grasped). Trials which were categorised as changes of mind are separated from direct reaches.

Of the 2906 trials which were of type (i) or type (ii), 1462 were targets on the left, and 1444 were targets on the right. However, the relative proportion of type (i) trials to type (ii) trials was unbalanced between left and right targets. 459 of the 1462 (31.4%) reaches to the left were initially in the wrong direction, while just 192 of the 1444 (13.3%) reaches to targets on the right initially went in the wrong direction.

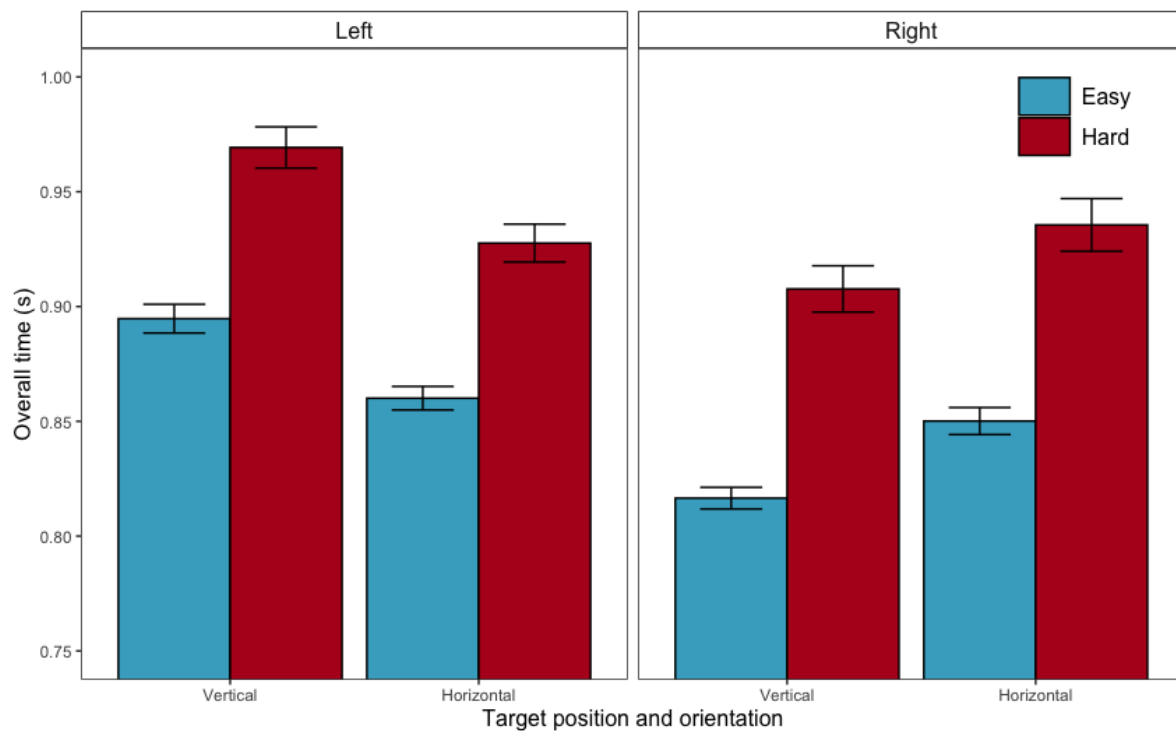
In this section, the outcome measures (i) overall time, (ii) initiation time, (iii) movement time, and (iv) curvature will be analysed for trials where the correct target was grasped and retrieved, whether or not there was a “change of mind” on the way. The timing variables were subjected to a negative reciprocal ( $-1/t$ ) transformation to meet model assumptions from which fixed effect estimates with 95% confidence intervals were estimated using the bootstrap. Because of the non-linear transformation to the timing variables, the timing differences for main effects are reported in the text as a guide.

#### *2.3.1.1 Experiment 1: Overall Time*

The overall reach time is measured from the opening of the occlusion screen to when the reach was considered to have stopped. As can be seen in Figure 2-5, there is a clear advantage for the easy choice condition trials. Accompanying statistics are taken from a linear mixed model with parameters as specified in Table 2-2, where the most parsimonious model explained variation in mean initiation time using main effects of trial difficulty, target side, target orientation, and the interaction of target side and orientation.



Figure 2-5 Overall time between trial start and grasp for experiment 1



Note. Mean overall reach time in experiment 1, separated across left and right reaches (left panel and right panel), and target orientations, with blue bars representing reaches made in easy-choice trials, and red bars representing reaches made in hard-choice trials. Error bars represent within participant standard error.

As expected, high perceptual uncertainty trials took longer to complete than trials with low uncertainty (back-transformed time difference = 0.071s,  $\beta=0.042$ , 95% CI [0.040, 0.045]). The timings presented in this chart include the time taken to perceive the targets, judge which to pick up, program the movement needed and execute the reach and grasp action. Of course, some of these stages are likely to occur in parallel.

Aside from trial difficulty, the reaches to the right reduced overall reach duration (difference = 0.021s,  $\beta=-0.026$ , 95% CI [-0.029, -0.024]) and reach duration to horizontal targets was trended shorter (difference = 0.001s,  $\beta=-0.001$ , 95% CI [-0.004, 0.002]). However, the interaction between target side and target orientation had a stronger influence ( $\beta=0.020$ , 95% CI [0.018, 0.023]): as can be seen in Figure 2-5, for leftward reaches it took participants longer to grasp the vertical target compared to a horizontal target, but this pattern was reversed for rightward reaches.

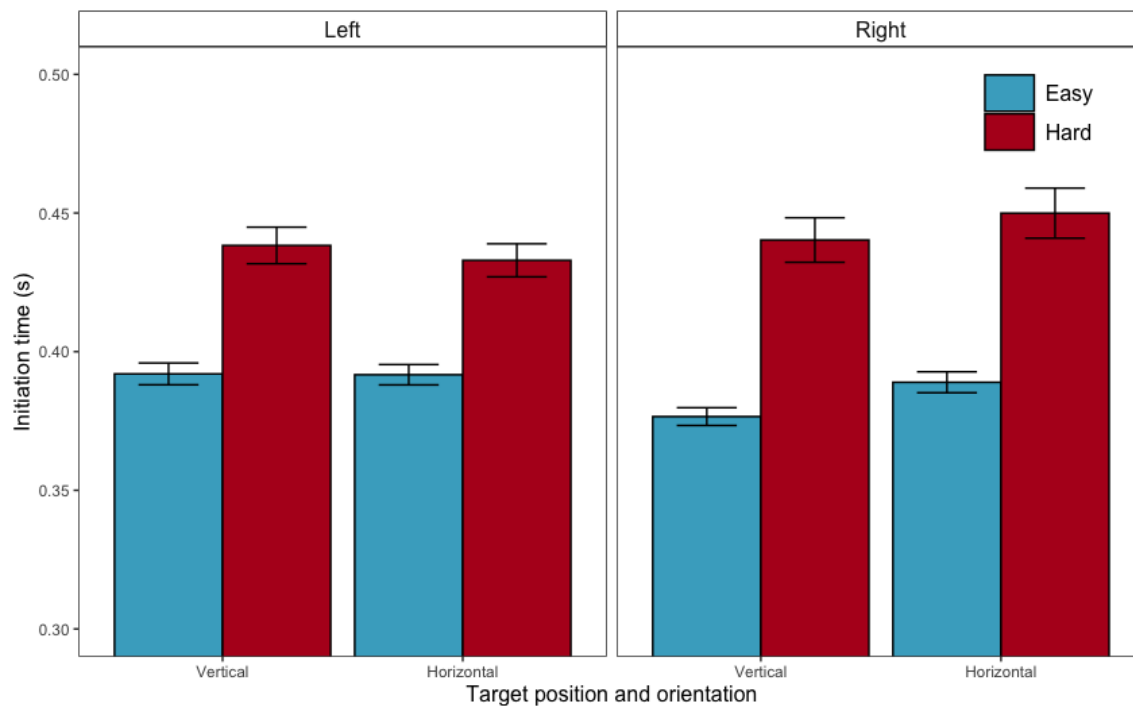
Of course, the overall time to grasp included the period between the trial starting and the reach motion initiating and the time it took to execute the reach and grasp. Isolating these components of the reach allow us to see whether the differences in overall time are due to relatively delayed initiation due to increased perceptual difficulty, or more time-consuming reaches-to-grasp movements.

#### *2.3.1.2 Experiment 1: Initiation Time*

Figure 2-6 and accompanying statistics in Table 2-2 shows that initiation times, that is the latency between the start of each trial and the start of the overt reach action, show expected differences between easy choice and hard choice trials (mean difference = 0.033s,  $\beta=0.108$ , 95% CI [0.100, 0.116]). There is also a marginally significant advantage, regardless of difficulty, for targets on the right (difference = 0.004s,  $\beta=-0.016$ , 95% CI [-0.024, -0.0008]). There is a statistically significant advantage for vertically oriented targets (difference = 0.005s,  $\beta=0.015$ , 95% CI [0.008, 0.023]), and an interaction between target side and orientation ( $\beta=0.017$ , 95%CI [0.009, 0.025]).

An increase in initiation time corresponds with expected effects of trial difficulty. The perceptual decision about which target was the correct one was more difficult, and participants took longer to make this decision. The influence of target side or orientation is less easy to explain on initiation times, but it is plausible that these effects are driven by relatively low-level factors, such as (right-)handedness and biomechanical constraints (see below).

Figure 2-6 Reach initiation time for experiment 1.



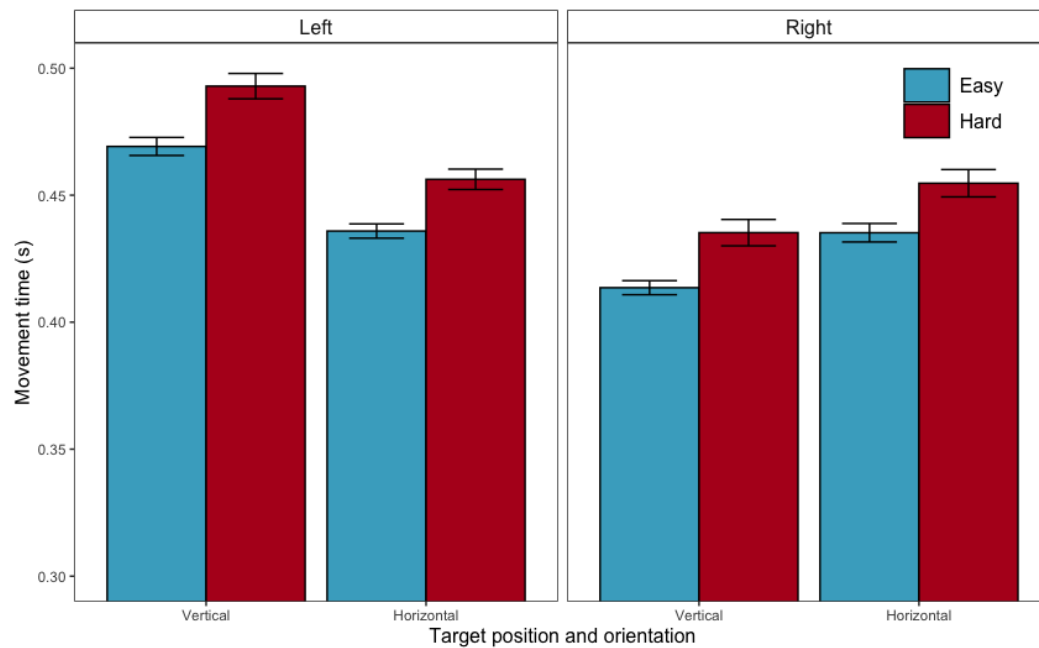
Note. Mean initiation time in experiment 1, separated across left and right reaches (left panel and right panel), and target orientations, with blue bars representing reaches made in easy-choice trials, and red bars representing reaches made in hard-choice trials. Error bars represent within participant standard error.

### 2.3.1.3 Experiment 1: Movement Time

Figure 2-7 and accompanying statistics in Table 2-2 show that movement time, from the initiation of the reach movement to when the grasp has been completed, shows similar effects of difficulty, target side and orientation. The influence of increased trial difficulty was less here (difference = 0.021s,  $\beta=0.043$ , 95% CI [0.038, 0.049]) than for initiation time (difference = 0.033s,  $\beta=0.108$ ), but as can be seen there remain main effects of target side (difference = 0.028s,  $\beta = -0.081$ , 95% CI [-0.086, -0.075]) and target orientation (difference = 0.032s,  $\beta=-0.010$ , 95% CI [-0.016, -0.005]) and the interaction between the two ( $\beta=0.067$ , 95% CI [0.061, 0.071]). As with overall time, the main location effect reflects that rightwards reaches take less time overall, and the interactions reflect that it takes longer overall to move to and grasp vertical targets on the left compared to horizontal targets, but on the right this pattern is reversed. In the statistical

model of movement time there was an effect of Distractor Congruency where reaches took less time when the distractor object had a different orientation to the target object (difference = 0.002s,  $\beta=-0.014$ , 95% CI [-0.019, -0.008]).

Figure 2-7 Movement time for experiment 1.



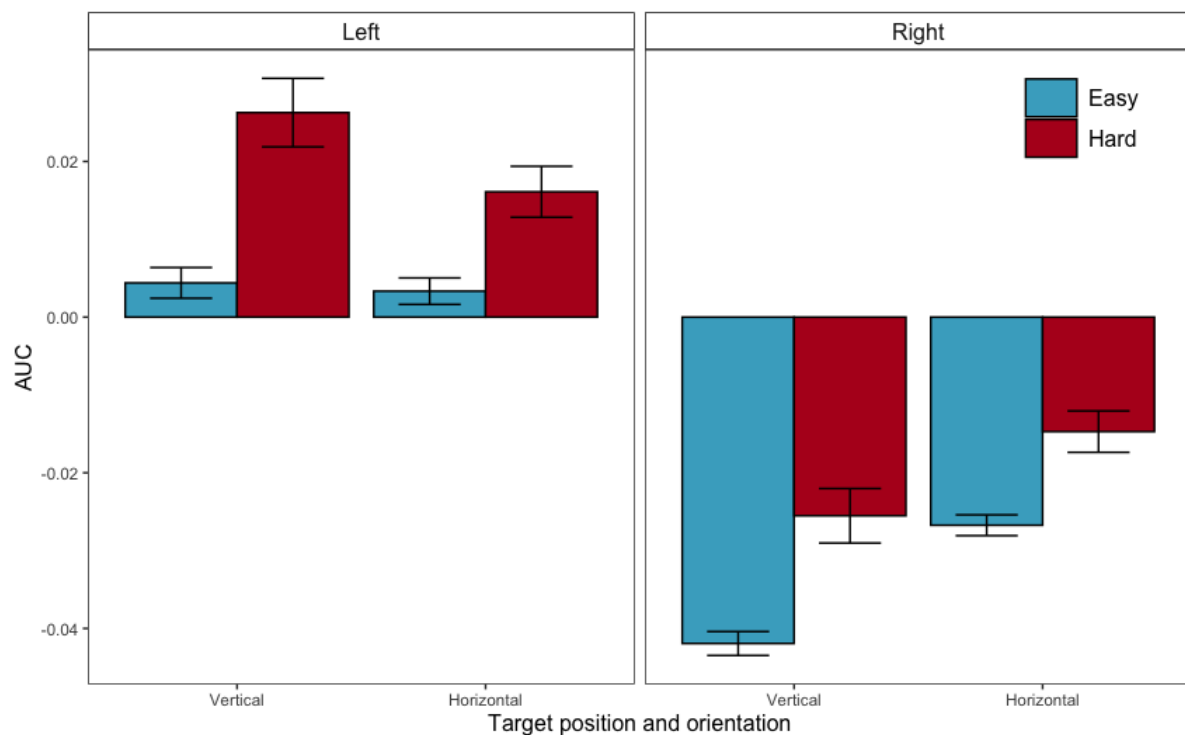
Note. Mean movement time in experiment 1, separated across left and right reaches (left panel and right panel), and target orientations, with blue bars representing reaches made in easy-choice trials, and red bars representing reaches made in hard-choice trials. Error bars represent within participant standard error.

The effects of target location and orientation and their interaction, could reflect more complex trajectories being needed to grasp targets that are more awkward to execute, requiring a more complex sequence of muscle activations (more on this below). The effect of difficulty will lead to longer reach paths if there is marked diversion towards the distractor or if reaches initiated with lower confidence had a decreased velocity (Dotan et al., 2019). Subsection 2.3.2.1 address the influence of such 'changes of mind' on this pattern of results.

### 2.3.1.4 Experiment 1: Curvature

Reach path curvature, measured as the area between the path of the knuckle from reach initiation to the grasp and the straight line between the starting position and final position of the knuckle marker, is shown in Figure 2-8. The Euclidean distance between the start and end positions is scaled to 1 and that curvature away from the non-target is given a negative sign. Therefore, a theoretical reach which extends in a straight line forwards to turn sharply to the target may have a value of about 0.2 area units (au), and a reach which might travel in a straight line all the way to the non-target before travelling to the target would have an area of 0.4 au (see Figure 2-4 for example trajectories and associated AUC measures).

Figure 2-8 Mean curvature as signed Area Under Curve



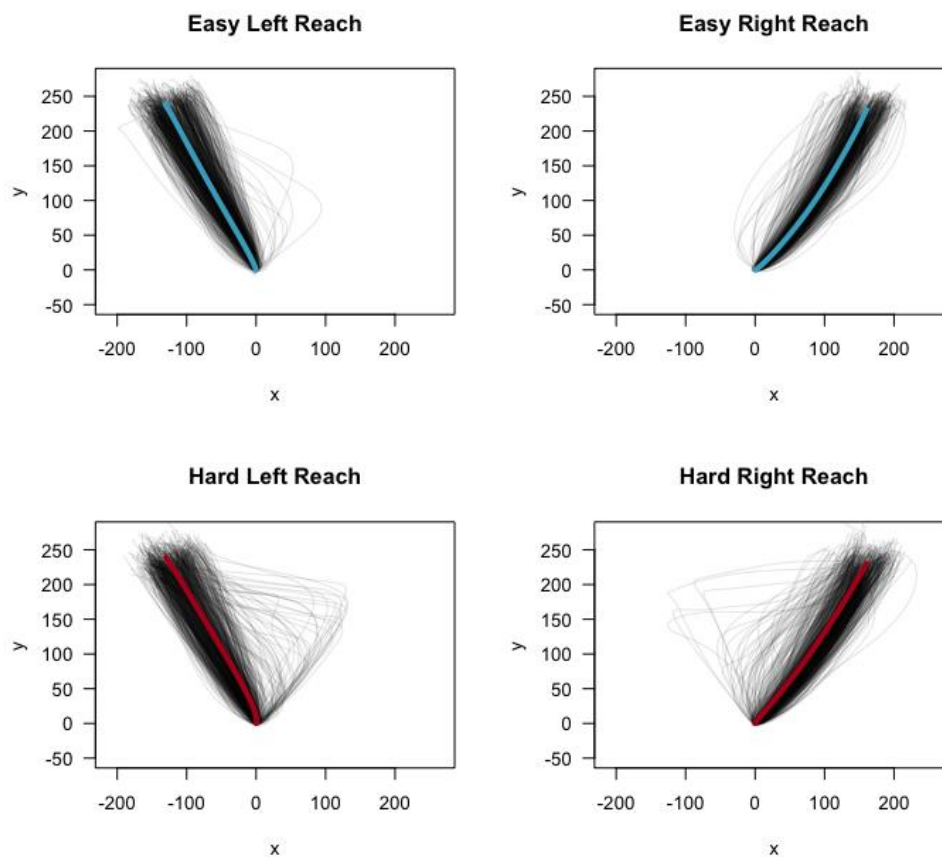
Note. Mean signed AUC in experiment 1, separated across left and right reaches (left panel and right panel), and target orientations, with blue bars representing reaches made in easy-choice trials, and red bars representing reaches made in hard-choice trials. Error bars represent within participant standard error

The mean curvature is more positive in the hard choice condition than the easy choice condition, with an increase in the AUC of 0.0079 au (95% CI [0.0070, 0.0088]). Regardless of difficulty, reaches towards the right have a much lower AUC (-0.0198, 95% CI [-0.0207, -0.0190]) due to

overall curvature being *away* from the non-target. Therefore, for difficult rightward targets, the pull towards the non-target actually results in a *straightening up* of the trajectory. Target orientation has a slight influence on mean AUCs (0.0019, 95% CI [0.0010, 0.0028]), but the interaction with target location is more robust (0.0046, 95% CI [0.0038, 0.0055]). For leftward reaches, the trajectories curve more towards the distractor for vertical targets compared to horizontal targets; for rightward reaches, the pattern flips in that reaches curve away from the non-target more for vertical targets.

To gain a better understanding of these results, it is useful to look at the raw path data recorded in the experiment. Figure 2-9 shows the mean path overlaid on all paths, for reaches toward left and right targets in the easy and hard choice conditions in experiment 1.

Figure 2-9 Experiment 1 Raw and Mean Trajectories

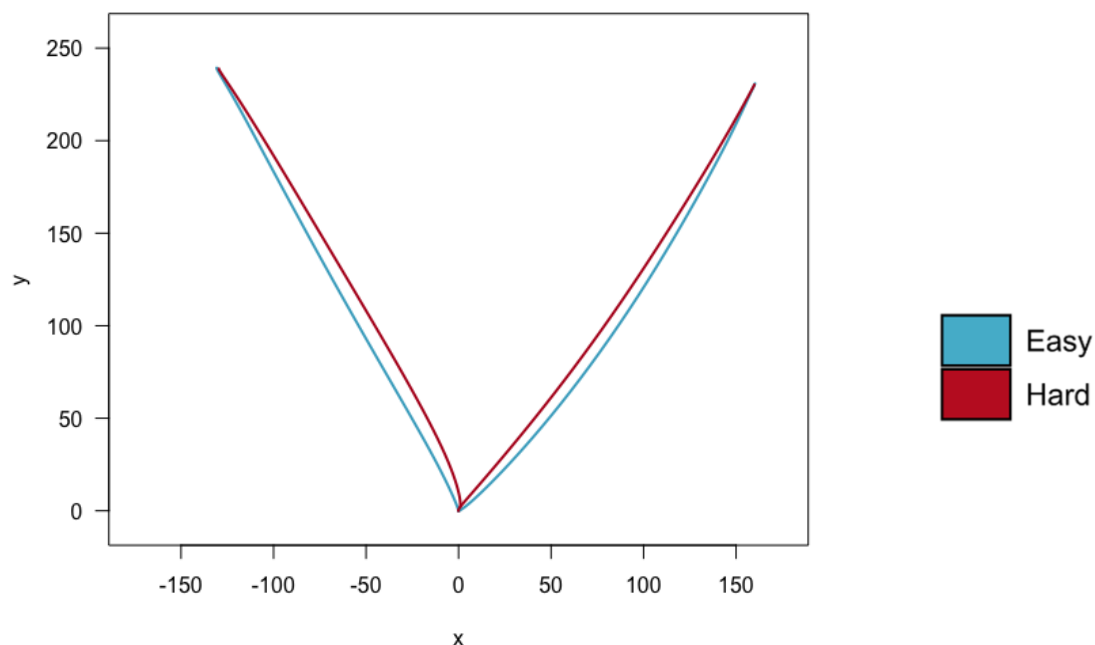


Note. The black lines are all the eventually correct reach paths recorded in the experiment, and the overlaid lines are the mean paths for each condition. The upper panels are the reaches made in the easy-choice condition, and the lower panels are the reaches made in the hard-choice condition. The left two panels are reaches to targets on the left,

and the right panels are reaches to targets on the right. All paths have been shifted so that they begin at the xy coordinate (0,0).

Because the calculation of AUC returns a negative value for paths which curve away from the distractor target, the mean AUC for difficult-choice reaches to targets on the right is closer to zero than the mean AUC for easy-choice reaches to targets on the right. A comparison of the mean trajectories can be seen in Figure 2-10. Taking these together an increase of choice difficulty increases the mean AUC value across trajectories recorded in experiment 1.

Figure 2-10 Mean reach paths in experiment 1, overlaid



Note. Mean reach paths recorded in experiment 1. Blue lines are the mean reach paths made in easy-choice trials, and red lines are the reaches made in hard-choice trials. For reaches to the left both easy-choice and hard-choice trials have a positive curvature (towards the distractor target), however easy and hard-reach trials to the right have a negative curvature (away from the distractor target).

### 2.3.2 Experiment 1: Statistical Analysis

Table 2-2 shows the regression weights from the final models for each outcome measure from experiment 1, each of which were constructed via backwards selection from a full model with all potential effects and their interactions.

Table 2-2 Regression Coefficients and Standard Errors of Fixed Effects for Each Outcome

## Measure in Experiment 1

Term in refined model	Outcome Measure			
	Overall Time (inverse)	Initiation Time (inverse)	Movement Time (inverse)	AUC (untransformed)
Random Effects:				
Participant Level Variance	0.12	0.33	0.3	0.011
Residual Variance	0.14	0.43	0.3	0.048
Fixed Effects:				
(Intercept)	-1.153 (0.021) ***	-2.565 (0.058) ***	-2.318 (0.053) ***	-0.0072 (0.0022) **
Difficulty	0.0428 (0.0026) ***	0.1081 (0.0079) ***	0.0432 (0.0055) ***	0.00788 (0.00089) ***
Target Side	-0.0262 (0.0026) ***	-0.0159 (0.0079) *	-0.0806 (0.0055) ***	-0.01983 (0.00089) ***
Target Orientation	-0.0010 (0.0026)	0.0158 (0.0079) *	-0.0104 (0.0055) +	0.00192 (0.00089) *
Target Side : Orientation	0.0202 (0.0026) ***	0.0169 (0.0079) *	0.0663 (0.0055) ***	0.00464 (0.00089) ***
Distractor Congruency	.	.	-0.0139 (0.0055) *	.
Full Model AIC	-2924.4	3562.8	1500.1	-9148.3
Final Model AIC	-3047.1	3460.5	1400.2	-9292.5

Note. Table shows the fixed effect and random effect parameters for overall time, initiation time, movement time and AUC for valid trials from experiment 1, after a backwards selection procedure from a fully interacting model. A negative reciprocal transform has been applied to the timing measures. The parameter estimates are shown with their standard error in parentheses.

Significance codes: \*\*\*  $p < 0.001$ , \*\*  $p < 0.01$ , \*  $p < 0.05$ , †  $p < 0.1$

In summary, difficulty exerted a clear and robust effect on all outcome measures, but after model selection there were no interactions between difficulty and the workspace variables. The workspace variables of target side and orientation affected each outcome measure. I speculate that these effects stem from lower-level factors such as handedness and biomechanics. I will return to this issue below after the presentation of Experiment 2.

### 2.3.2.1 Experiment 1: Analysis with “changes of mind” excluded.

A subset of trials from all participants were categorised as “change of mind” trials, where the reach path initially travelled towards the distractor, before eventually grasping the correct target (see section 2.2.6). Change of mind trials are an obvious source of outlier trials and they occur



more frequently in the difficult condition (185 easy choice trials vs. 280 hard choice trials). A reasonable question is to what extent the effects of difficulty on the various outcome measures are driven by these extreme trials. Therefore, the mixed-effects analyses were repeated after removing changes of mind trials from the data. The results are shown in Table 2-3.

Table 2-3 Regression Coefficients and Standard Errors for Each Outcome Measure in Experiment 1, With Change of Mind Trials Excluded.

Term	Overall Time (inverse)	Initiation Time (inverse)	Movement Time (inverse)	AUC (untransformed)
Random Effects:				
Participant Level Variance	0.12	0.33	0.3	0.011
Residual Variance	0.13	0.42	0.27	0.023
Fixed Effects:				
(Intercept)	-1.168 (0.021) ***	-2.565 (0.059) ***	-2.367 (0.054) ***	-0.019 (0.002) ***
Difficulty	0.0367 (0.0028) ***	0.111 (0.009) ***	0.0226 (0.0056) ***	.
	-0.0193 (0.0029)		-0.0689 (0.0057)	
Target Side	***	-0.0031 (0.0091)	***	-0.0147 (0.0005) ***
	-0.00017 (0.00283)			
Target Orientation	(ns)	.	-0.0052 (0.0056)	0.00274 (0.00049) ***
Difficulty x Target Side	0.0081 (0.0028) **	0.021 (0.009) *	.	.
Target Side x Target Orientation	0.0199 (0.0028) ***	.	0.0657 (0.0056) ***	0.00430 (0.00049) ***
Distractor Congruency	.	.	-0.0130 (0.0056) *	.
Full Model AIC	-2376.3	2746.0	727.5	-10269.5
Final Model AIC	-2488.8	2642.6	629.1	-10439.4

Note. Table shows the fixed effect and random effect parameters for overall time, initiation time, movement time and AUC for valid trials from experiment 1, after a backwards selection procedure from a fully interacting model. A negative reciprocal transform has been applied to the timing measures. The parameter estimates are shown with their standard error in parentheses.

Significance codes: \*\*\* p < 0.001, \*\* p < 0.01, \* p < 0.05, † p < 0.1

Without change of mind trials, the effect of difficulty is still present in all timing measures, but not in curvature. For overall time, movement time and curvature, the estimate for the effect of difficulty is reduced (or eliminated) when change of mind trials are removed. This change is to be expected as the change of mind trials will typically trace a longer path, and thus be both slower

overall. For the initiation time measure, the coefficient for the effect of difficulty is greater once changes of mind have been removed. It is plausible that change of mind trials reflect a group of fast initial errors that are corrected before the grasp is completed. These initial errors will have occurred more often in the difficult condition, so removing them increases the effect of difficulty on initiation time. That the effect of increased perceptual choice difficulty is no longer in the statistical model to explain variation in curvature, possibly indicates that participants may not have been executing reaches with target location interference. However, to explore further how AUC measurements may be related to difficulty in the subset of trials without change of minds, recall that the incidence of change of mind trials was different between reaches to targets on the left and the right. This imbalance may have led to more subtle effects of difficulty on curvature being obscured. As can be seen in Table 2-4, there is an effect of trial difficulty on AUC in reaches to the right, but not for reaches to the left. For reaches to the left, there is an interaction between trial difficulty and target orientation. This indicates that removing change of mind trials from the analysis may not have completely removed the effect of difficulty on path curvature.

Table 2-4 Influential factors on mean AUC, experiment 1

Term	AUC both sides, no changes of mind	AUC left reaches, no changes of mind	AUC right reaches, no changes of mind
Random Effects			
Participant Level Variance	0.011	0.015	0.017
Residual Variance	0.023	0.021	0.018
Fixed Effects			
(Intercept)	-0.019 (0.002) ***	-0.0028 (0.0027)	-0.0336 (0.0031) ***
Difficulty	.	-0.00014 (0.00068)	0.00134 (0.00052) *
Target Side	-0.0147 (0.0005) ***	NA	NA
Target Orientation	0.00274 (0.00049) ***	-0.00146 (0.00069) *	0.00756 (0.00052) ***
Target Side x Target Orientation	0.00430 (0.00049) ***	NA	NA
Difficulty x Target Orientation	.	-0.00155 (0.00068) *	.
AIC	-10439.4	-4723.4	-6296

Note. Table shows the fixed effect and random effect parameters for AUC for valid trials from experiment 1, after a backwards selection procedure from a fully interacting model. The first column is analysis applied to AUC for trials to

the left target and right target combined, and the latter two columns are based on the data split across left-target reaches and right-target reaches. The parameter estimates are shown with their standard error in parentheses.

Significance codes: \*\*\*  $p < 0.001$ , \*\*  $p < 0.01$ , \*  $p < 0.05$ , †  $p < 0.1$ .

In this first experiment I have established that increasing the difficulty of the perceptual choice between reach targets affects several temporal and spatial movement parameters. These findings suggest that the decision dynamics identified with process-tracing methods, such as mouse-tracking (e.g. Freeman & Ambady, 2010), do generalise in some way to naturalistic reach-to-grasp movements.

Recall that in mouse-tracking, participants are frequently encouraged to initiate movements quickly. By making sure that the movement starts while the underlying decision process is unfolding, that movement may provide a better, moment-to-moment reflection of the underlying decision process. Therefore, in Experiment 2 a time pressure mechanism was introduced in order to maximise the influence of the underlying decision dynamics on the reaching movement.

### 2.3.3 Experiment 2

For the second experiment reported in this chapter, a time pressure manipulation was added using a switch under the starting position which was released when participants started movement. This manipulation was successful in reducing the latency of initiation times across both difficulty conditions and the gap between those, as well as increasing the proportion of “change of mind” trials (see below for details).

If a participant had not started movement within 400ms of the trial start, an aversive buzzer sound was triggered once the trial was over. This movement deadline was intended to encourage early movement, so 400ms was chosen because it was close to the average initiation time for easy choice trials in experiment 1. This time limit is similar to the stimulus onset to

initiation requirements in previous motor plan studies (Chapman et al., 2010; Wong & Haith, 2017). The number and percentage of trials that breached this limit for the experiment overall are shown in Table 2-5. Some participants struggled to consistently meet this target and Table 2-6 shows the mean number of trials triggered before the deadline across participants, as well as the range. Because of this trials that were not initiated within this time limit were retained.

Table 2-5 Count and proportion of reaches initiated before 400ms

Choice Condition	Correct Reaches		Incorrect Reaches		Total
	Direct	CoM	Direct	CoM	
Easy	724 (59.5%)	112 (68.3%)	2 (100%)	1 (100%)	839 (60.3%)
Hard	575 (60.7%)	206 (67.9%)	54 (54.5%)	22 (56.4%)	857 (60.2%)

Note. Table shows the counts of all trials from experiment 2 which were launched before the 400ms time limit was breached, divided across trial difficulty, and whether the reach was correct or incorrect and a direct reach or a change of mind reach.

Table 2-6 Mean and range of reach initiations before 400ms

Choice Condition	Correct Reaches		Incorrect Reaches	
	Direct	CoM	Direct	CoM
Easy	25.0 (3-41)	3.86 (0-13)	0.07 (0-1)	0.03 (0-1)
Hard	19.8 (1-33)	7.10 (1-19)	1.86 (0-7)	0.76 (0-4)

Note. Table shows the mean number of trials that each participant launched before the 400ms time limit, with the range of trials in each category across participants .

In all other respects data processing for experiment 2 was the same as experiment 1. Out of all 2784 trials (29 participants completing 96 trials), motion tracking errors led to three trials being dropped from analysis, one from the easy condition and two from the hard condition. None of the remaining trials took more than two seconds from the trial start to detection of the reach.

Across participants, the average number of completely correct trials was 74.9 (range: 53-88); the average number of trials which were correct with a change of mind average was 16.2 (range: 7-38); the average number of trials that each participant picked up the wrong block without diverting was 4.0 (range: 1-9); finally, the average number of incorrect trials with change of mind average was 2.1 (range 1-6). Note that time pressure had no strong influence on the overall error rate, with only three trials removed from the easy condition from a total of 1391 (compared to six in experiment 1) and 138 trials were removed from the hard condition from a

total of 1390 (compared to 110 in experiment 1). There was a similar proportion of change of mind trials in the easy choice condition (12.1% for experiment 1, and 11.8% for experiment 2), but a slight increase in the proportion of change of mind trials in the hard choice condition (18.3% for experiment 1 and 28.6% for experiment 2). Of the 2640 trials which were either directly correct or correct after a change in direction (types (i) and (ii)), 1313 were targets on the left, and 1327 were targets on the right. However, the relative proportion of type (i) trials to type (ii) trials was unbalanced between left and right targets. 468 of the 1313 (35.6%) reaches to the left were initially in the wrong direction, while just 212 of the 1327 (16.0%) reaches to targets on the right initially went in the wrong direction.

Table 2-7 Count and proportion of trajectory types recorded in Experiment 2

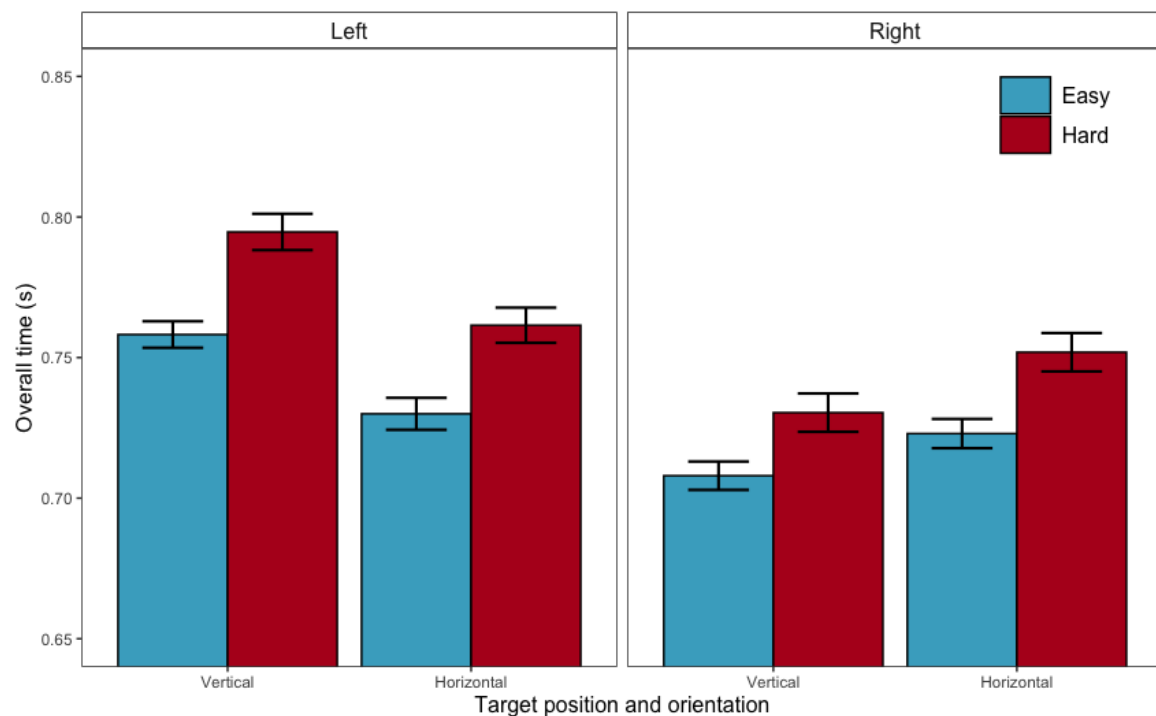
Choice Condition	Correct Reaches (tot. = 2640)		Incorrect Reaches (tot. = 141)		Total
	Direct	CoM	Direct	CoM	
Easy	1104 (79.7%)	284 (20.4%)	1 (0.1%)	2 (0.1%)	1391
Hard	854 (61.4%)	398 (28.6%)	100 (7.2%)	38 (2.7%)	1390
Total	1958 (70.4%)	682 (24.5%)	101 (3.6%)	40 (1.4%)	2781

Note. Table shows the total count and proportion of trials from experiment 2 which were correct or incorrect and direct or changes of mind.

### 2.3.3.1 Experiment 2: Overall Time

Figure 2-11 shows the average overall reach time (made up of initiation and movement times), averaged over participants. As reported in Table 2-8, trials in the hard choice condition took longer to complete than trials with low uncertainty (difference = 0.028s,  $\beta=0.024$ , 95% CI [0.021, 0.027]). It also took participants less time overall to reach and grasp targets on the right (difference = 0.016s,  $\beta=-0.032$ , 95% CI [-0.035, -0.029]). There is an interaction between target side and orientation, where vertical targets are picked up faster than horizontal targets if they are on the left, and slower than horizontal targets if they are on the right ( $\beta=0.022$ , 95% CI [0.019, 0.025]), which is supported by a marginally significant advantage for vertical targets ( $\beta=-0.0047$ , 95% CI [-0.0076, -0.0018]).

Figure 2-11 Overall time between trial start and grasp for experiment 2. Error bars represent within participant standard error.



Note. Mean overall reach time in experiment 2, separated across left and right reaches (left panel and right panel), and target orientations, with blue bars representing reaches made in easy-choice trials, and red bars representing reaches made in hard-choice trials. Error bars represent within participant standard error.

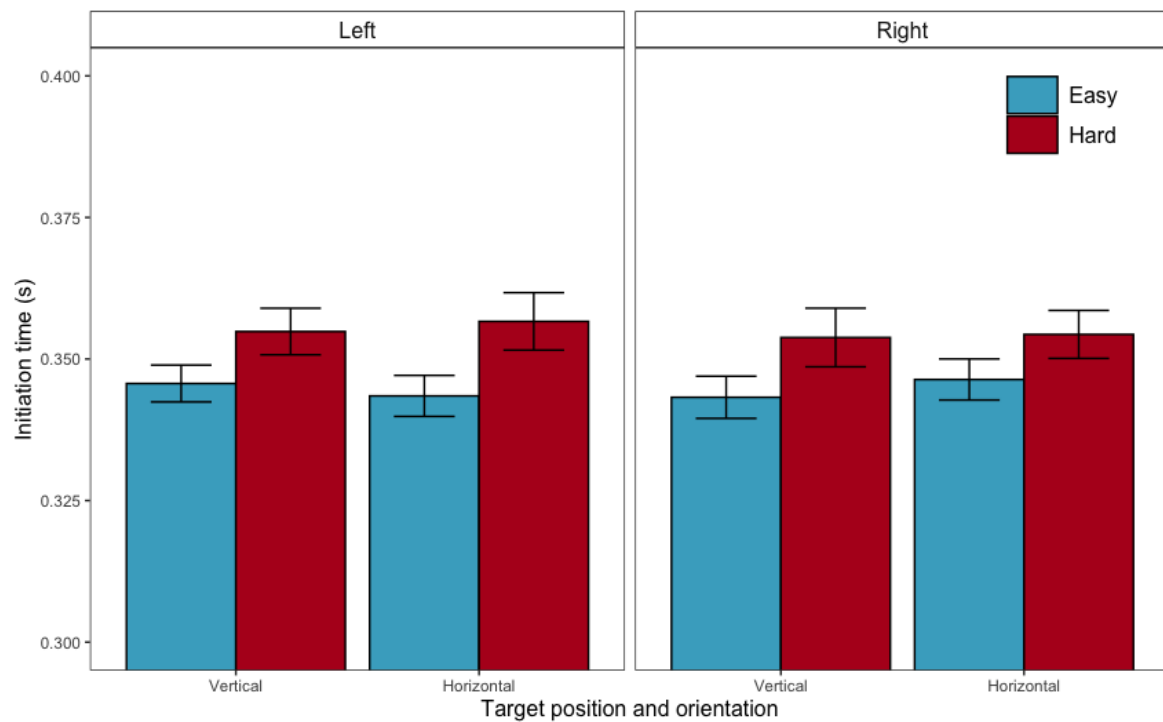
There were no further interactions remaining after backwards elimination from the full model.

Reaches took longest to pick up vertical targets on the left, and the least amount of time to pick up vertical targets on the right. In comparison to experiment 1, participants in experiment 2 were quicker on overall time measures for every combination of factors.

### 2.3.3.2 Experiment 2: Initiation Time

In experiment 2, initiation times across target locations and orientations are very similar as can be seen in Figure 2-12. The only effect remaining after backwards elimination is that of trial difficulty (time difference = 0.006s,  $\beta=0.026$ , 95% CI [0.018, 0.035]). There are none of the small but significant position or interaction effects from experiment 1. The more complex pattern of *overall* reach timings therefore come from the movement phase of the trials, with the effect of difficulty being equivalent regardless of reach location and target orientation.

Figure 2-12 Reach initiation time for experiment 2.



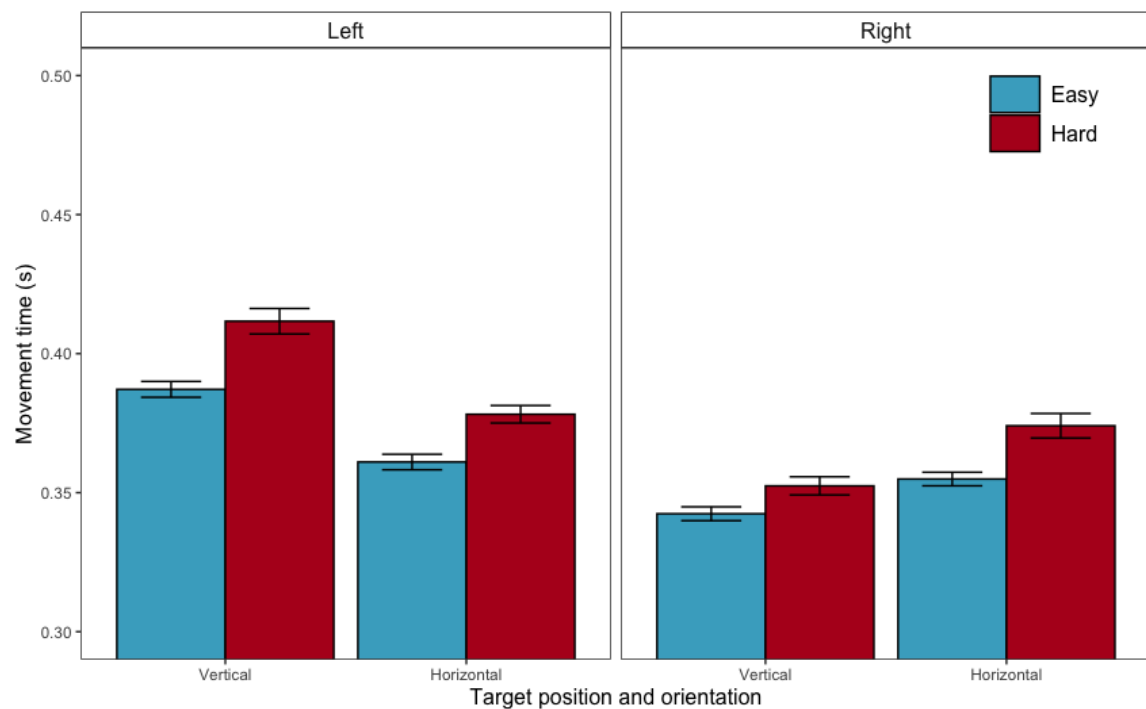
Note. Mean initiation time in experiment 2, separated across left and right reaches (left panel and right panel), and target orientations, with blue bars representing reaches made in easy-choice trials, and red bars representing reaches made in hard-choice trials. Error bars represent within participant standard error.

### 2.3.3.3 Experiment 2: Movement Time

Average movement times from experiment 2 are displayed in

Figure 2-13 and show that increased trial difficulty has a strong effect on how long reaches took to execute (difference = 0.016s,  $\beta=0.059$ , 95% CI [0.052, 0.065]), though this is less of a difference than from experiment 1 (0.021s). Reach direction mattered (difference = 0.027s,  $\beta=-0.109$ , 95% CI [-0.116, -0.102]), as did target orientation (difference = 0.04s,  $\beta=-0.015$ , 95% CI [-0.022, -0.008]) as did the interaction effect ( $\beta=0.078$ , 95% CI [0.072, 0.086]).

Figure 2-13 Movement time for experiment 2, error bars represent within participant standard error



Note. Mean movement time in experiment 2, separated across left and right reaches (left panel and right panel), and target orientations, with blue bars representing reaches made in easy-choice trials, and red bars representing reaches made in hard-choice trials. Error bars represent within participant standard error.

Overall, the average reach time to vertical targets on the right was shortest while reaches to vertical targets on the left were longest. Horizontal target reaches were more similar, but with a time advantage to targets on the right. Differences in reach timing to differently oriented targets in the same location are probably due to the grasp orientation requiring a different approach vector and a slightly different arm position from which to start the grasp phase of the movement. In comparison to experiment 1, average movement times were all shorter in experiment two, indicating that the time saving between the experiments were due to faster initiation *and* reach execution.

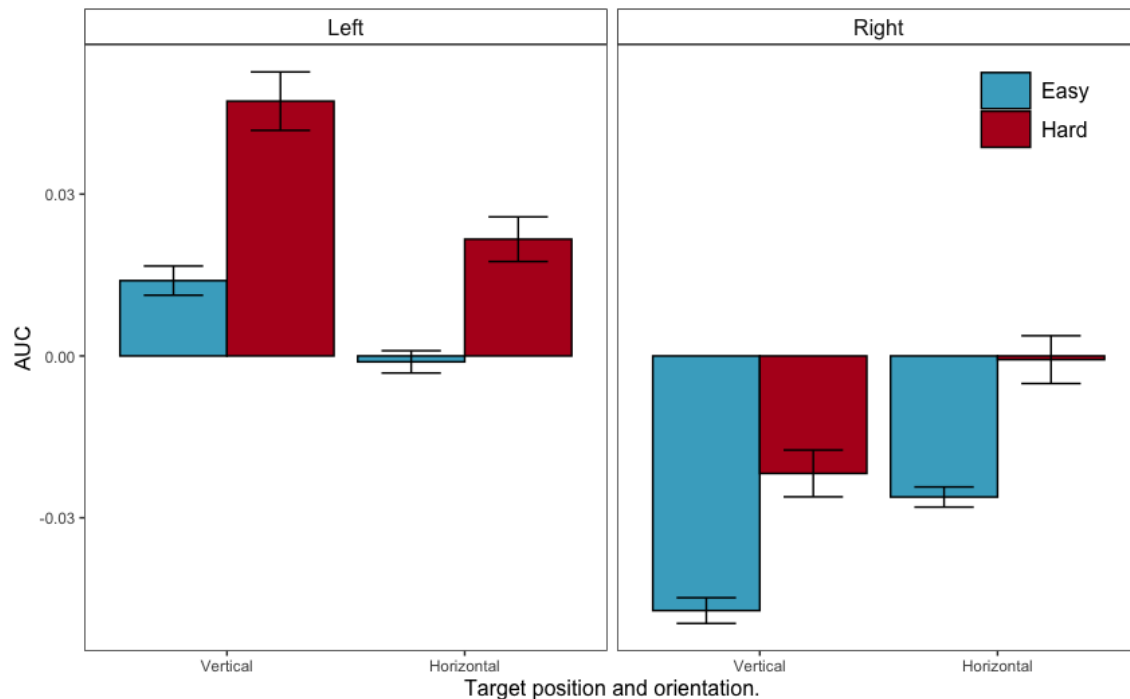
#### 2.3.3.4 Experiment 2: Curvature Analysis

As can be seen in Figure 2-14, an increase in trial difficulty increased mean AUC ( $\beta=0.0136$ , 95% CI [0.012, 0.015]) and, relative to leftward reaches, AUCs for right side targets were more



negative ( $\beta=-0.022$ , 95% CI  $[-0.023, -0.021]$ ). There was a strong interaction between target side and target orientation for curvature ( $\beta=0.010$ , 95% CI  $[0.009, 0.012]$ ), but no main effect for target orientation ( $\beta=0.0004$ , 95% CI  $[-0.001, 0.002]$ ).

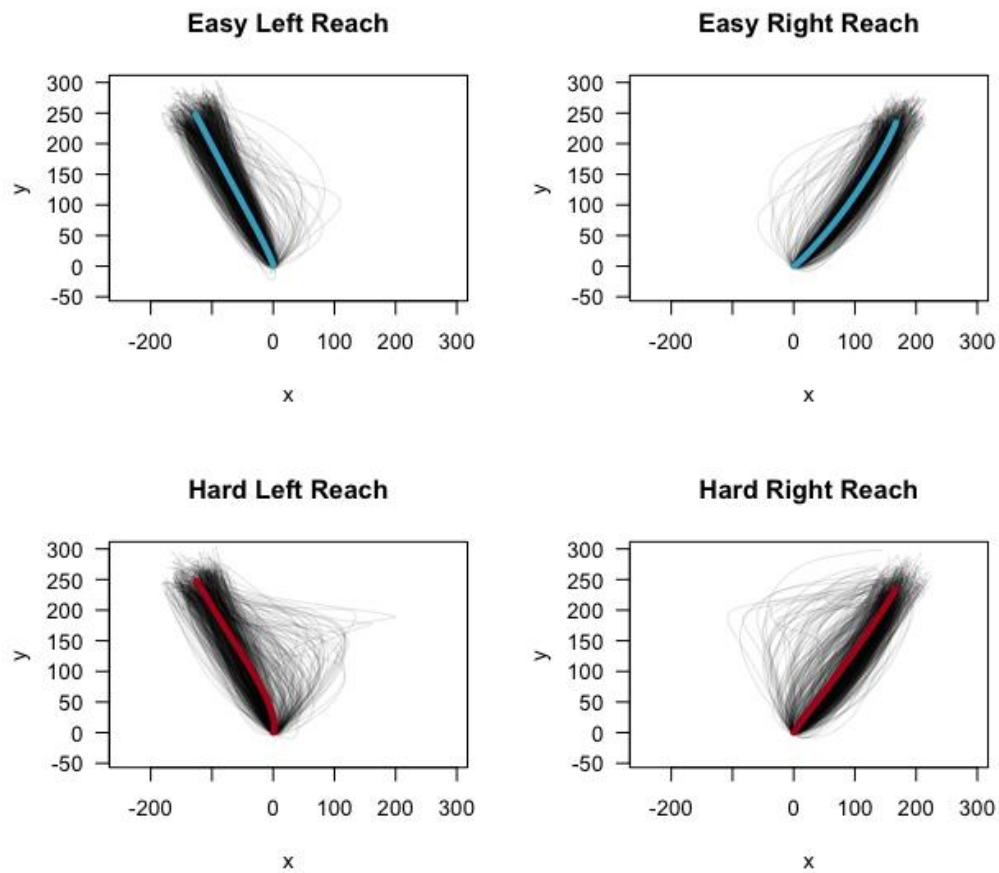
Figure 2-14 Mean curvature as signed Area Under Curve, error bars represent within participant standard error.



Note. Mean signed AUC in experiment 1, separated across left and right reaches (left panel and right panel), and target orientations, with blue bars representing reaches made in easy-choice trials, and red bars representing reaches made in hard-choice trials. Error bars represent within participant standard error.

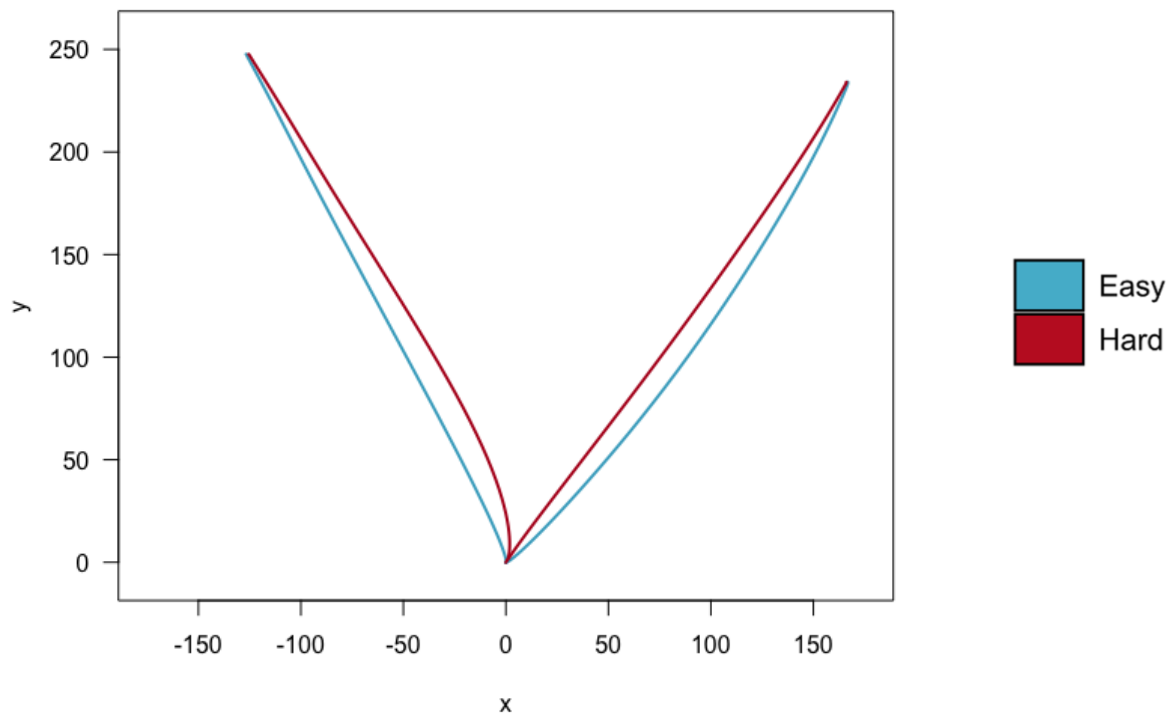
The curvature analysis shows an approximately doubled effect of difficulty on curvature in comparison to experiment 1. Interestingly, easy reaches to targets on the right have stronger absolute curvature but also a shorter reach time. The robust simple effect of difficulty on movement time but not in curvature suggests that a more complex relationship between movement velocity and perceptual difficulty may be occurring in these data than longer reaches simply taking more time to execute. The overall negative curvature, particularly for easy reaches to the right, can be seen in Figure 2-15, and Figure 2-16 shows how the mean path changes between the easy trials in blue, and the hard trials in red.

Figure 2-15 Experiment 2 Raw and Mean Trajectories



Note. The black lines are all the eventually correct reach paths recorded in the experiment, and the overlaid lines are the mean paths for each condition. The upper panels are the reaches made in the easy-choice condition, and the lower panels are the reaches made in the hard-choice condition. The left two panels are reaches to targets on the left, and the right panels are reaches to targets on the right. All paths have been shifted so that they begin at the xy coordinate (0,0).

Figure 2-16 Mean reach paths in experiment 2



Note. Mean reach paths recorded in experiment 2. Blue lines are the mean reach paths made in easy-choice trials, and red lines are the reaches made in hard-choice trials. For reaches to the left both easy-choice and hard-choice trials have a positive curvature (towards the distractor target), however easy and hard-reach trials to the right have a negative curvature (away from the distractor target).

### 2.3.4 Experiment 2: Statistical Analysis

Table 2-8 shows the regression weights after the backwards selection procedure was applied to the data from experiment two. Difficulty maintained its robust effect across all outcome measures. For overall time there were additional influences of target orientation both alone and in interaction with target side. The addition of the time pressure on initiation times reduced the magnitude of the difficulty effect. For movement time and reach path curvature workspace effects continued to be influential. As with experiment 1, an analysis without the “change of

mind” trials may be informative about whether there are more subtle effects of difficulty over and above the insertion of changes of mind into the responses made by participants.

Table 2-8 Regression Coefficients and Standard Deviations of Random Effects and Standard Errors of Fixed Effects for Each Outcome Measure in Experiment 2

Term	Overall Time (inverse)	Initiation Time (inverse)	Movement Time (inverse)	AUC (untransformed)
Random Effects:				
Participant Level Variance	0.14	0.3	0.42	0.014
Residual Variance	0.15	0.45	0.34	0.06
Fixed Effects:				
(Intercept)	-1.379 (0.026) ***	-2.973 (0.056) ***	-2.823 (0.079) ***	-0.0017 (0.0029)
Difficulty	0.0236 (0.0029) ***	0.0268 (0.0088) **	0.0568 (0.0066) ***	0.0134 (0.0012) ***
Target Side	-0.0316 (0.0029) ***	.	-0.1103 (0.0066) ***	-0.0222 (0.0012) ***
Target Orientation	-0.0055 (0.0029) +	.	-0.0176 (0.0066) **	0.00021 (0.00116)
Target Side x Target Orientation	0.0221 (0.0029) ***	.	0.0770 (0.0066) ***	0.0103 (0.0012) ***
Distractor Congruency	.	.	.	0.00063 (0.00116)
Difficulty x Target Orientation	.	.	.	-0.0013 (0.0012)
Difficulty x Distractor Congruency	.	.	.	-0.00084 (0.00116)
Target Orientation x Distractor Congruency	.	.	.	7.3e-05 (1.2e-03)
Difficulty x Target Orientation x Distractor Congruency	.	.	.	0.0024 (0.0012) *
Full Model AIC	-2259.3	3482.1	2023.0	-7050.6
Final Model AIC	-2379.2	3356.4	1918.9	-7192.7

Note. Table shows the fixed effect and random effect parameters for overall time, initiation time, movement time and AUC for valid trials from experiment 2, after a backwards selection procedure from a fully interacting model. A negative reciprocal transform has been applied to the timing measures. The parameter estimates are shown with their standard error in parentheses.

Significance codes: \*\*\* p < 0.001, \*\* p < 0.01, \* p < 0.05, † p < 0.1.

#### 2.3.4.1 Experiment 2: Analysis with “Change of Mind” trials excluded

Similar to experiment 1, it is reasonable to ask to what extent the effects of difficulty are driven by the population of change of mind trials. There was a slight increase in the overall percentage of change of mind trials from experiment 1 to 2 (15.2% to 16.9%), showing that the time pressure increased the incidence of reach actions initiated before the competition for target selection was resolved. Table 2-9 shows the statistical output for these data.

Table 2-9 Regression coefficients and standard deviations of random effects and standard errors of fixed effects for the models with "change of mind" trials removed and after backwards selection

Term	Overall Time (inverse)	Initiation Time (inverse)	Movement Time (inverse)	AUC (untransformed)
Random Effects:				
Participant level variance	0.15	0.28	0.46	0.014
Residual variance	0.14	0.44	0.29	0.026
Fixed Effects:				
(Intercept)	-1.395 (0.027) *** 0.0141 (0.0033)	-2.950 (0.055) ***	-2.891 (0.082) ***	-0.0221 (0.0026) ***
Difficulty	*** -0.0325 (0.0034)	0.031 (0.010) **	0.0201 (0.0067) ** -0.1042 (0.0068)	0.00155 (0.00059) **
Target Side	***	-0.024 (0.010) *	***	-0.0167 (0.0006) *** 0.00266 (0.00059)
Target Orientation	0.0011 (0.0033)	.	0.0015 (0.0066)	***
Target Side x Target Orientation	0.0164 (0.0033) ***	.	0.0640 (0.0066) ***	0.00757 (0.00059) ***
Distractor Congruency	.	-0.024 (0.010) *	.	.
Full Model AIC	-1668.2	2408.3	922.2	-8054.0
Final Model AIC	-1786.3	2303.5	817.8	-8224.9

Note. Table shows the fixed effect and random effect parameters for overall time, initiation time, movement time and AUC for valid and direct trials from experiment 2, after a backwards selection procedure from a fully interacting model. A negative reciprocal transform has been applied to the timing measures. The parameter estimates are shown with their standard error in parentheses.

Significance codes: \*\*\*  $p < 0.001$ , \*\*  $p < 0.01$ , \*  $p < 0.05$ , †  $p < 0.1$

Removing the change of mind trials from these data did not eliminate the effect of difficulty from any outcome measure. Small significant effects emerged after this step, such as the influence of target side changing the initiation time for reaches Overall, it appears that the effects of difficulty on the various measures are not just driven by a relatively small proportion of extreme, change-of-mind trials. It is not just initial errors of reach direction that increase curvature, but perhaps “attraction” to the non-target.

### 2.3.5 Comparison of Experiments 1 and 2.

Comparing the results of experiments 1 and 2, we can see that there are consistent effects of the perceptual uncertainty manipulation most outcome measures. In terms of error rates these were broadly similar, but as intended the addition of the time manipulation slightly increased

the average number of “correct change of mind trials” from 14.8 to 16.2. The time manipulation changed some effects seen in the statistical analysis in experiment 2 compared to experiment 1 and these are detailed below.

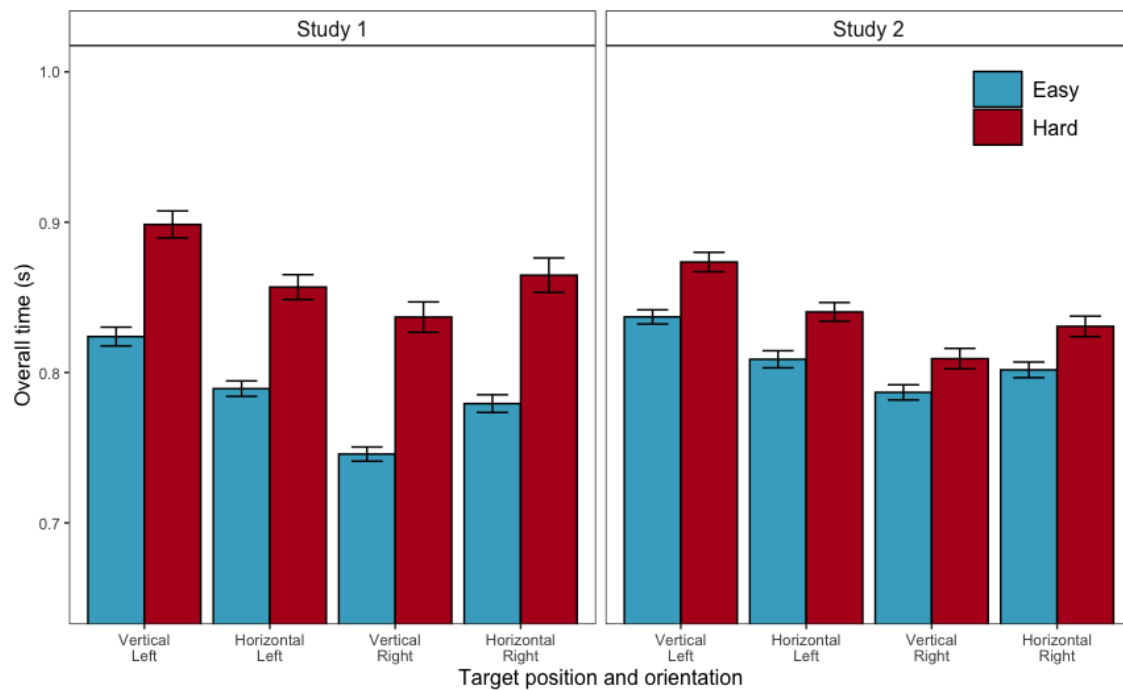
#### *2.3.5.1 Overall Time*

The overall reach time records the latency between the trial start, when the targets were revealed to the participants, and the end of the reach motion, when participants grasped the target. Included in this time is the necessary processing of the perceptual features of the stimuli (location, orientation, and luminance), the decision about which is the correct target, motor programming for the reach, and the execution of the reach-to-grasp motion, which may or may not happen in parallel with selection and planning.

The overall reach timing from trial start to the end of the reach was consistently influenced by difficulty, and can clearly be seen in Figure 2-17 and Figure 2-18. Trials with a more difficult perceptual decision took more time in both experiments. The addition of the time pressure manipulation in experiment 2 narrowed the difference between overall reach time between the easy and hard choice trials. Target side and orientation also had a strong effect on overall reach timing, with the interaction between these factors and the simple effect of target orientation remaining as strong influences after the time pressure manipulation was added in experiment 2.

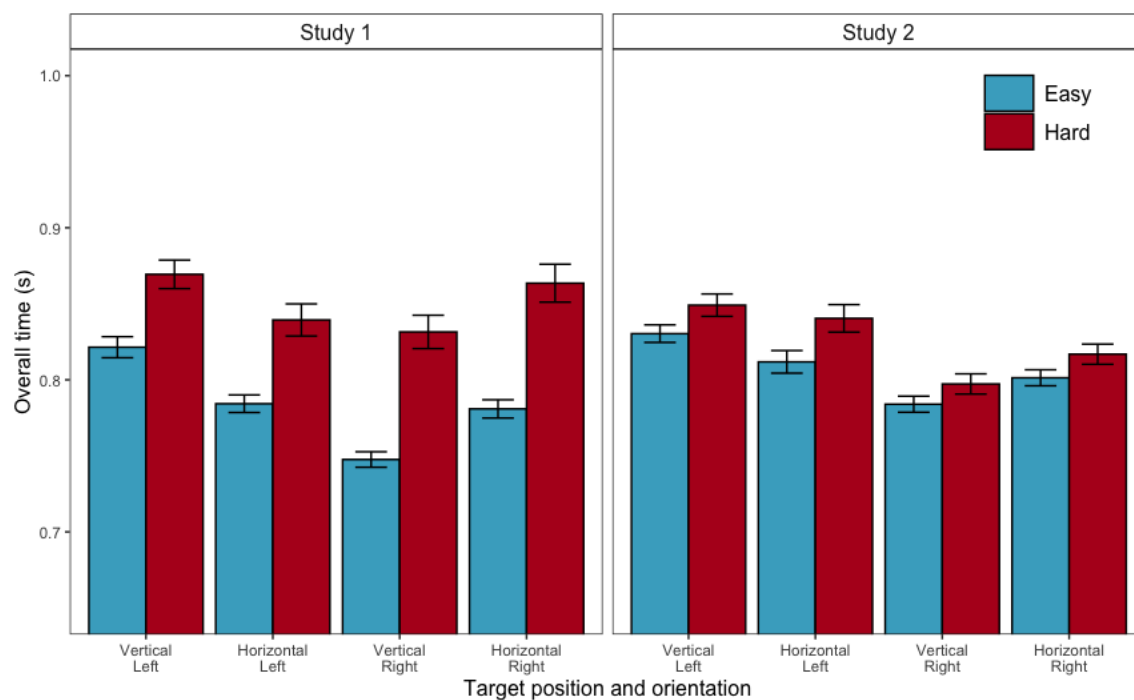
When “change of mind” trials were removed, the effect of difficulty on overall time remained in both experiments 1 and 2. The effect of target orientation alone and in interaction with target side also remained. In experiment 1 there was an interaction between target side and difficulty that did not “survive” into the analysis of results in experiment 2. A small effect of distractor congruency emerged in the results of experiment 2. As highlighted above, the overall reach time is informative about participant efficiency when executing the whole task, but these data can be broken down into initiation time and movement time.

Figure 2-17 Overall reach times in both experiments



Note. The mean overall reach time for all correct trials from experiments 1 and 2. Easy choice trials are in blue, and hard choice trials are in red. Trials are split according to the study, the target side, and the target orientation. Error bars represent within participant standard error.

Figure 2-18 Overall reach time for both experiments, without change of mind trials



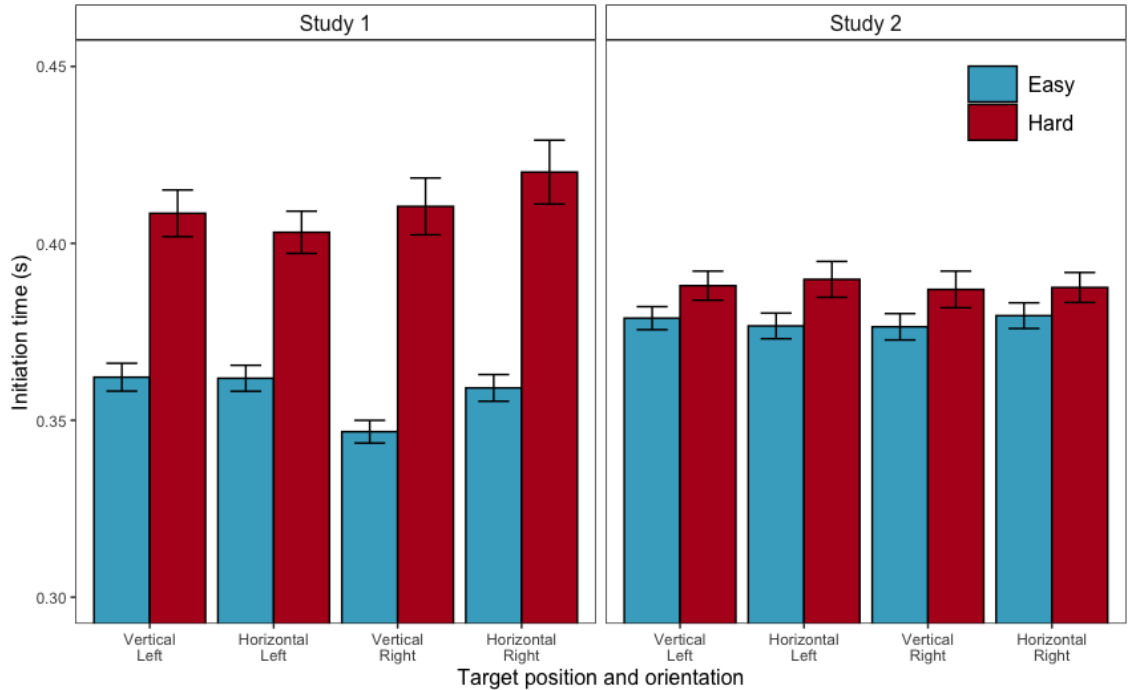
Note. The mean overall reach time for all correct and direct trials from experiments 1 and 2. Easy choice trials are in

blue, and hard choice trials are in red. Trials are split according to the study, the target side, and the target orientation. Error bars represent within participant standard error.

2.3.5.2 *Initiation Time*

Reach initiations were influenced by difficulty across both experiments 1 and 2. As can be seen in Figure 2-19 the addition of the time pressure manipulation in experiment 2 reduced, but did not eliminate, the difference in initiation times. Variability introduced by target side and target orientation seen in the results of experiment 1 did not appear in the results for experiment 2.

Figure 2-19 Initiation time in both experiments

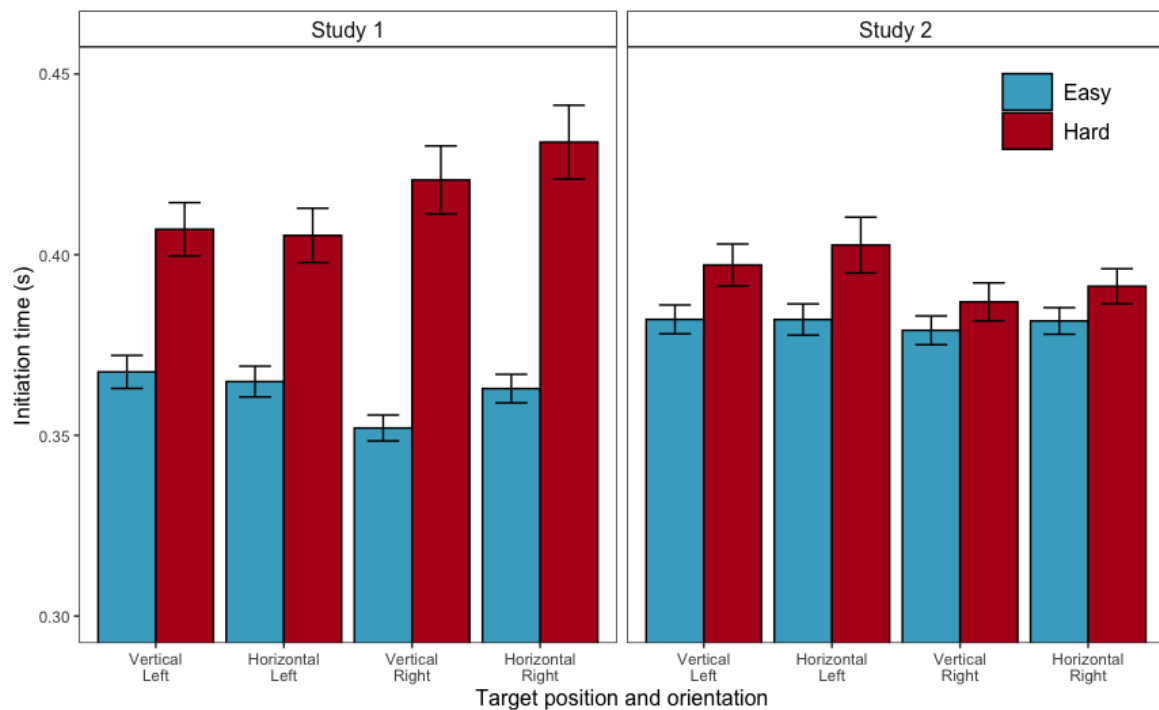


Note. The mean reach initiation time for all correct trials from experiments 1 and 2. Easy choice trials are in blue, and hard choice trials are in red. Trials are split according to the study, the target side, and the target orientation. Error bars represent within participant standard error.

However, when “change of mind” trials were excluded from the data from experiment 2, an effect of target side did appear as an explanatory variable for differences in the reach initiation timings, as did an effect of distractor congruency. Figure 2-20 presents these data visually.



Figure 2-20 Initiation time in both experiments, without change of mind trials

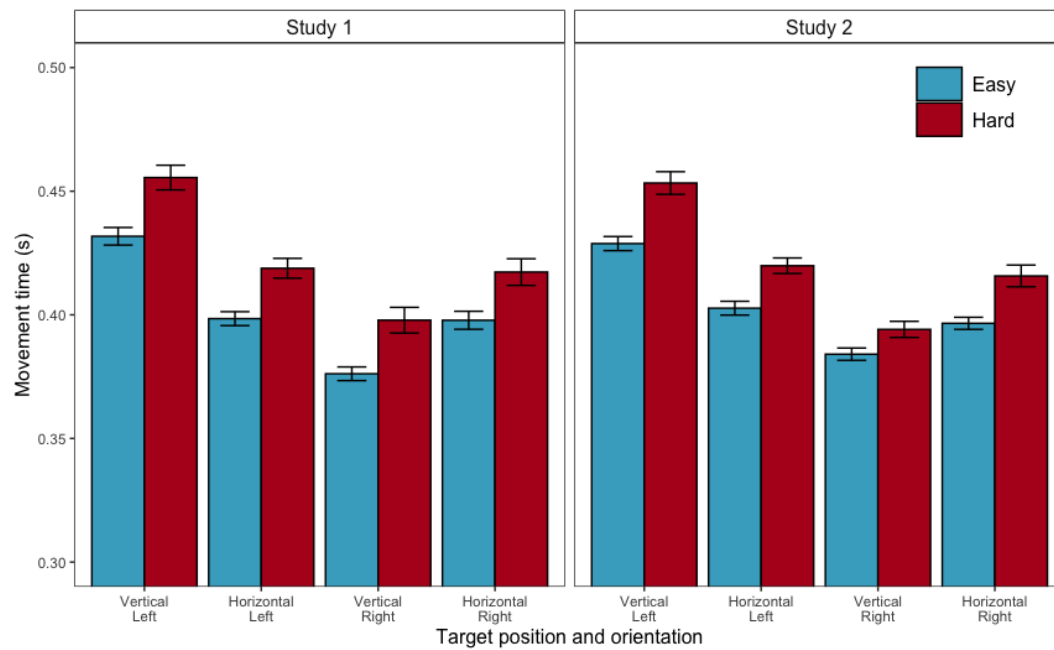


Note. The mean reach initiation time for all correct and direct trials from experiments 1 and 2. Easy choice trials are in blue, and hard choice trials are in red. Trials are split according to the study, the target side, and the target orientation. Error bars represent within participant standard error.

### 2.3.5.3 Movement Time

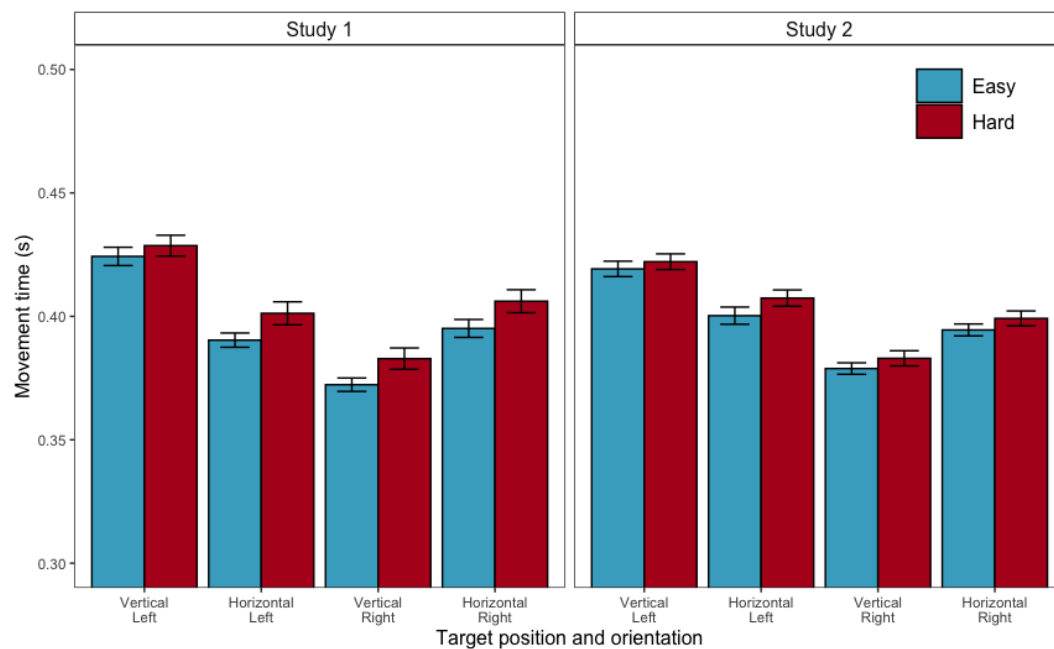
The time between reach initiation and grasping of the target was consistently affected by difficulty (increasing reach times for “hard” trials) and, separately, by target side and orientation, whether or not there was time pressure on the reach initiation. Removing “change of mind” trials reduced the effect of difficulty in experiment 1 but did little to the influences of target side and orientation in experiment 1, a pattern mostly replicated in experiment 2. The change in movement time between experiments can be seen in Figure 2-21 and Figure 2-22.

Figure 2-21 Movement time for both experiments



Note. The mean reach movement time for all correct trials from experiments 1 and 2. Easy choice trials are in blue, and hard choice trials are in red. Trials are split according to the study, the target side, and the target orientation. Error bars represent within participant standard error.

Figure 2-22 Movement time for both experiments, with changes of mind removed

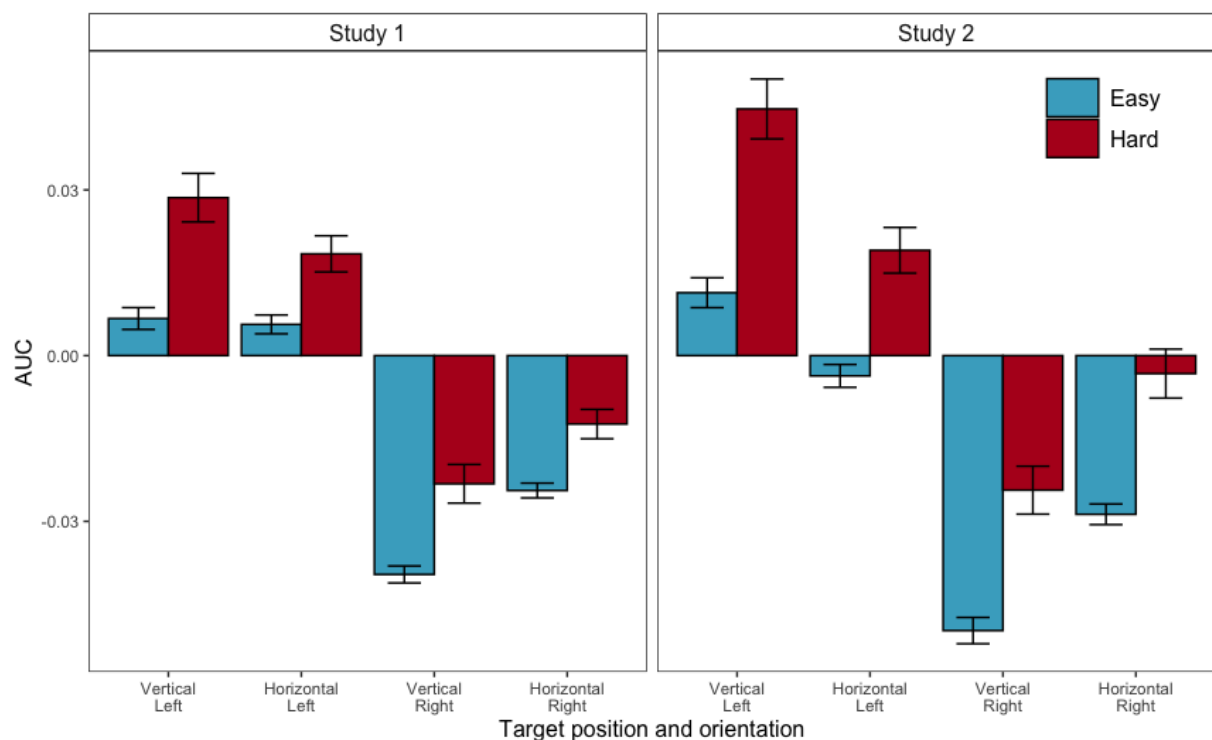


Note. The mean reach movement time for all correct and direct trials from experiments 1 and 2. Easy choice trials are in blue, and hard choice trials are in red. Trials are split according to the study, the target side, and the target orientation. Error bars represent within-participant standard error.

#### 2.3.5.4 Curvature

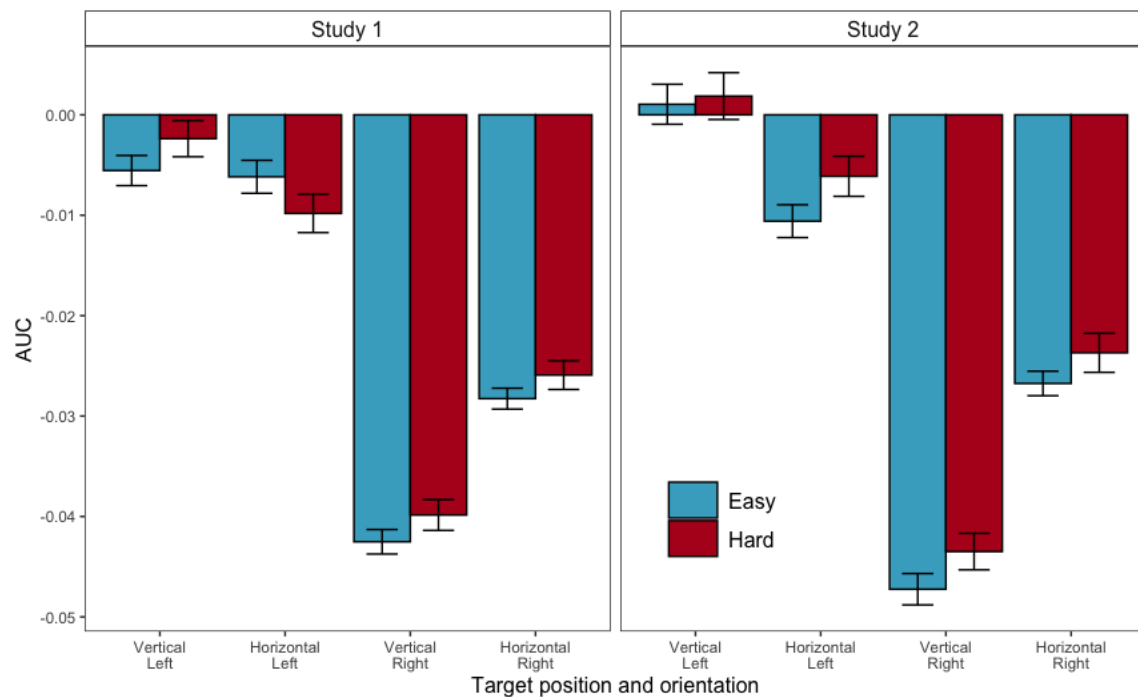
Experiments 1 and 2 both showed significant predictors of trial difficulty, target side, and the interaction between target side and orientation on movement curvature, and a visual comparison can be made with Figure 2-23. In experiment 1 there was no simple effect for target orientation, but there was an interaction effect between trial difficulty and target orientation, whereas in experiment 2 there was no interaction between difficulty and orientation, but there was a simple effect of orientation. The effect of difficulty was greater in experiment 2, reflecting, at least, the larger number of “change of mind” trials. Comparing curvature between experiments 1 and 2 after the “change of mind” trials were removed, trial difficulty retained some influence on mean curvature values in the statistical analyses. A visual comparison of the mean AUC values (Figures 2-23 and 2-24), demonstrates this influence.

Figure 2-23 Curvature values for both experiments



Note. The mean AUC for all correct trials from experiments 1 and 2. Trials are split according to the study, the target side, and the target orientation. Easy choice trials are in blue, and hard choice trials are in red. Trials are split according to the study, the target side, and the target orientation. Error bars represent within-participant standard error.

Figure 2-24 Curvature values for both experiments, with changes of mind removed



Note. The mean AUC for all correct and direct trials from experiments 1 and 2. Easy choice trials are in blue, and hard choice trials are in red. Trials are split according to the study, the target side, and the target orientation. Error bars represent within-participant standard error.

When change of mind trials are removed from these data, the mean AUC value for each combination of trial difficulty, target side, and target orientation is usually negative, indicating that on average the reaches recorded in the experiment curved away from the distractor item.

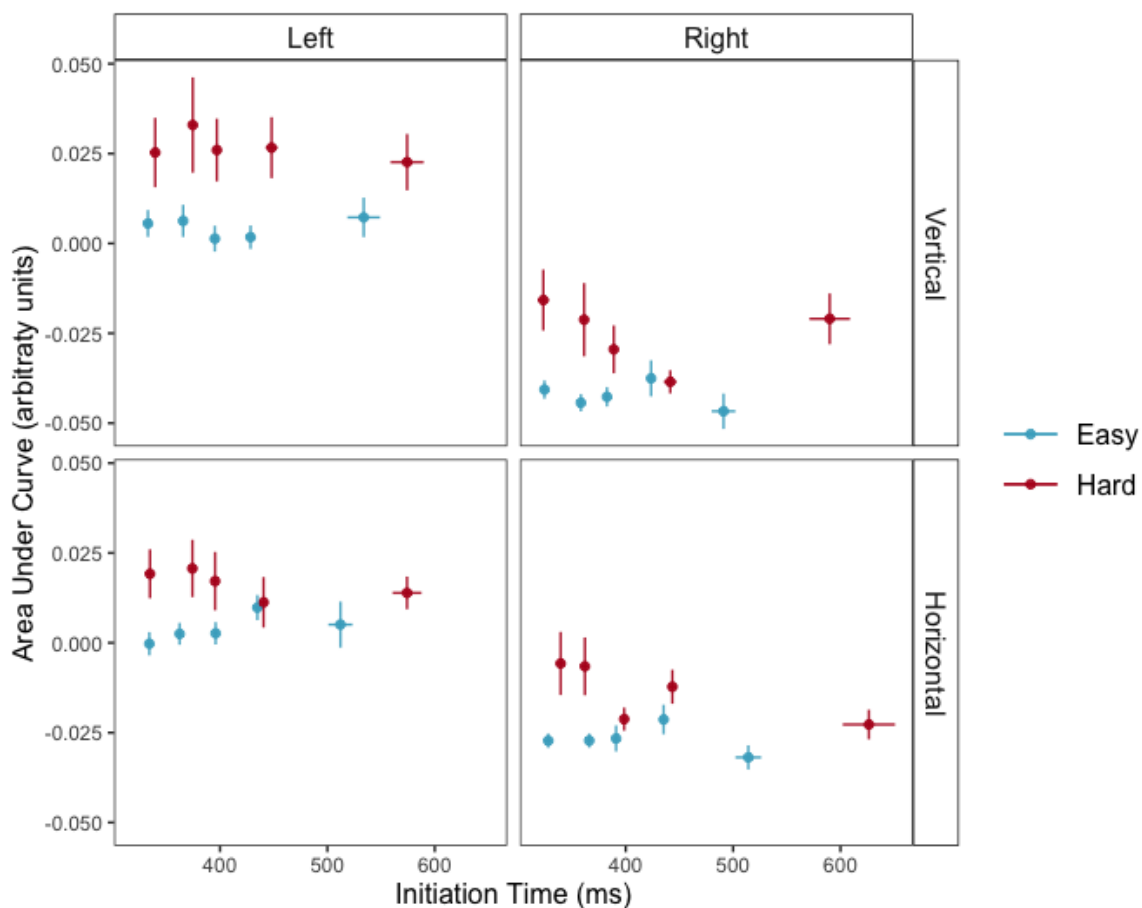
### 2.3.6 Workspace effects

Throughout the analyses reported above it was necessary to include the workspace factors of target side and target orientation to absorb variance and more precisely estimate the influence of trial difficulty. Across both experiments interactions between the difficulty of the perceptual decision and the location or orientation of the target only rarely impacted on the recorded reach timing and reach curvature metrics.

### 2.3.7 Relationships between curvature and timing variables

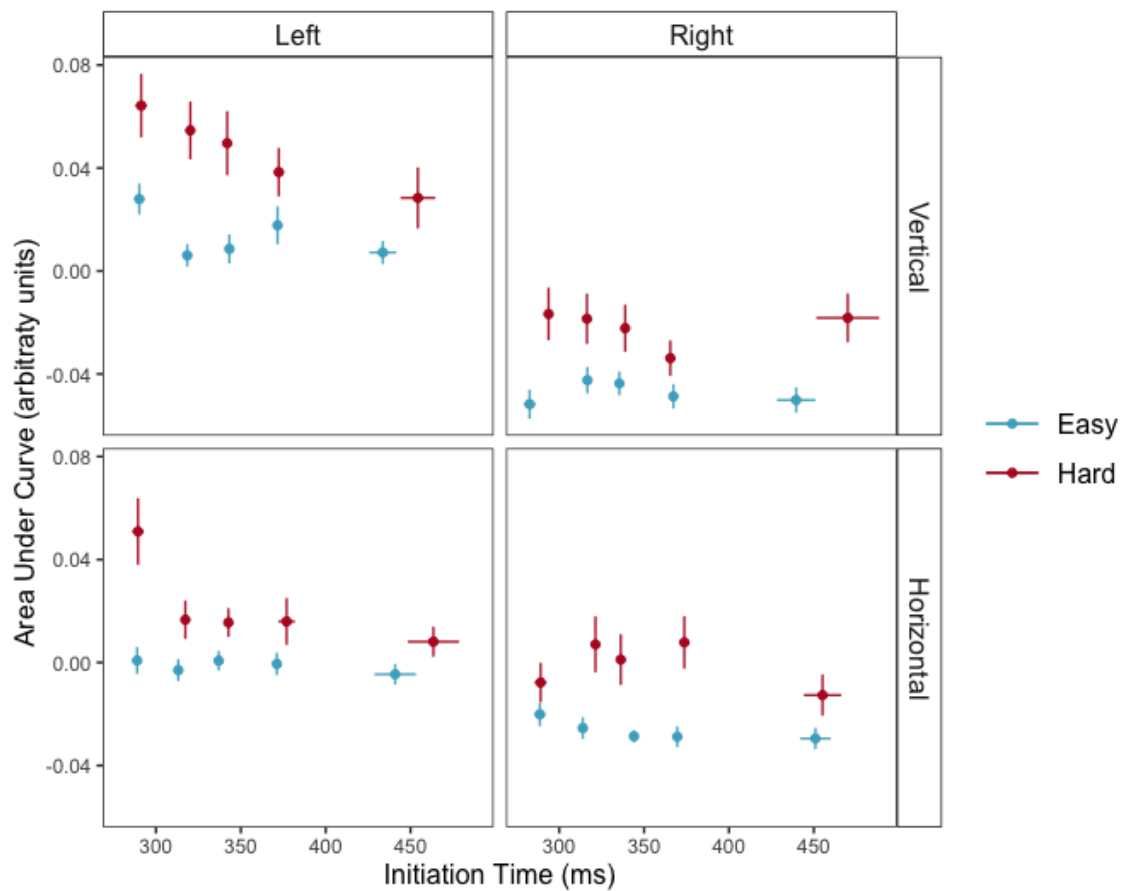
Removal change of mind trials from the analyses of experiments 1 and 2 changed the parameter estimates for how perceptual choice difficulty and workspace effects influenced reach timing and reach curvature. To examine these changes more closely, we can explore how the differences in curvature change between shorter and longer initiation times, and shorter and longer movement times. Figure 2-25 shows the mean AUC for each quintile of initiation time for experiment 1 and demonstrates a trend for a larger difference in AUC value for early reaches, which narrows with longer initiation times, but this trend is less evident for reaches to left targets which are vertically oriented.

Figure 2-25 Experiment 1 initiation time quintile and AUC plot



Note. Trials were divided by initiation time quintile (<20%, 20-40%, 40-60%, 60-80%, >80%) for each participant, trial difficulty, target side and orientation. Points are the mean initiation time for each quintile on the x-axis, and the mean AUC on the y-axis. Horizontal error bars are the within-participant standard error for initiation time, and the vertical error bars are the within-participant standard error for AUC. Easy choice trials are in blue, and hard choice trials are in red.

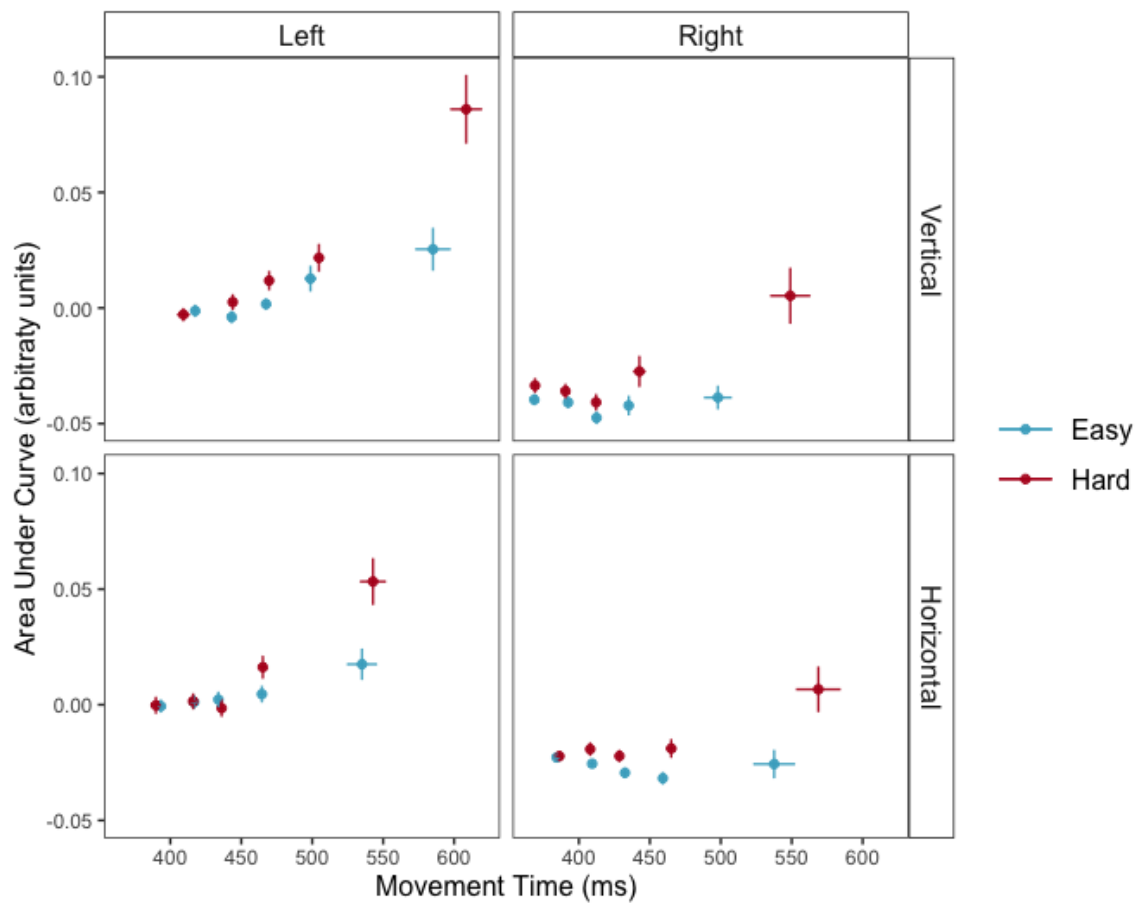
Figure 2-26 Experiment 2 initiation time quintile and AUC plot



Note. Trials were divided by initiation time quintile (<20%, 20-40%, 40-60%, 60-80%, >80%) for each participant, trial difficulty, target side and orientation. Points are the mean initiation time for each quintile on the x-axis, and the mean AUC on the y-axis. Easy choice trials are in blue, and hard choice trials are in red. Horizontal error bars are the within-participant standard error for initiation time, and the vertical error bars are the within participant standard error for AUC.

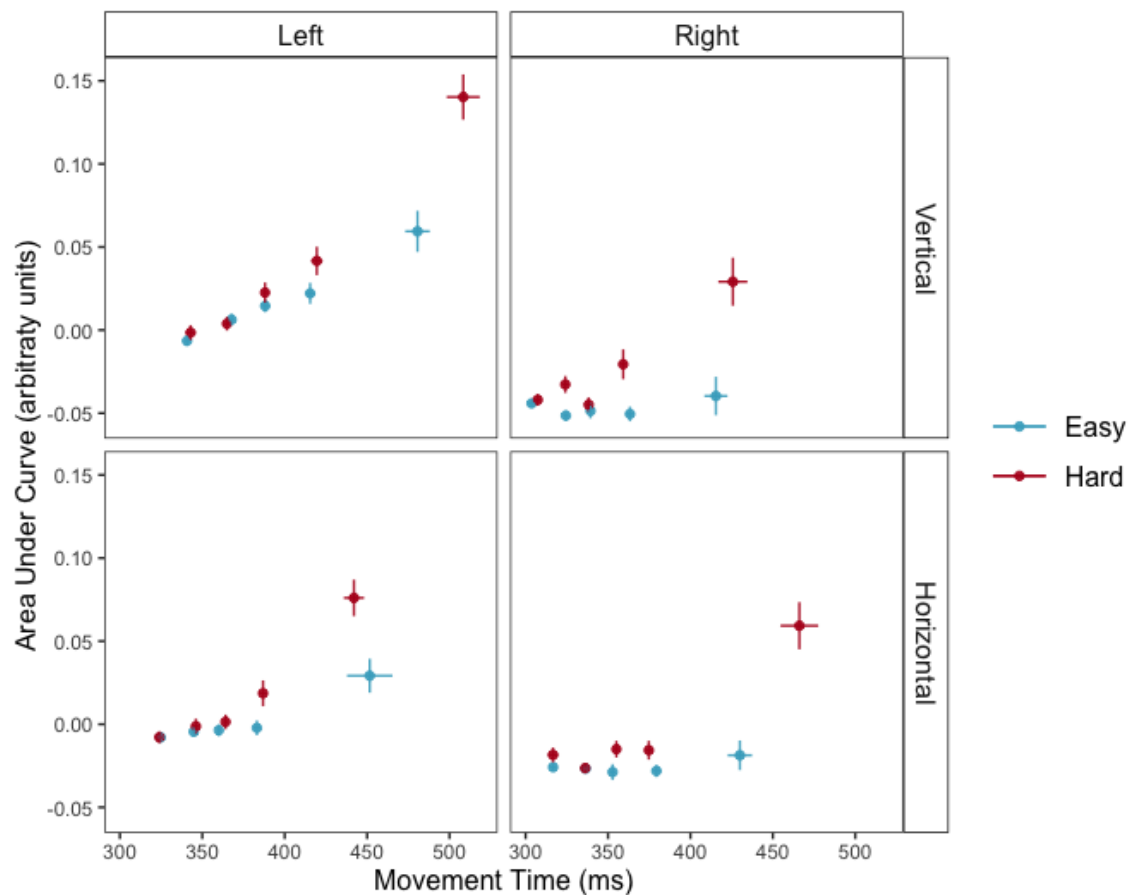
The relationship between movement time and curvature is plotted in Figure 2-27 and Figure 2-28 and shows the obvious: movements with a large degree of curvature took longer. For the reaches which were shorter, there was no systematic difference in curvature or movement speed, indicating that these actions were, perhaps, unchanged by choice processes. As movement time increases there is a separation between easy choice trials and difficult choice trials, with reaches made in the hard-choice condition showing more attraction to the distractor target, or at least less curvature away from the distractor target.

Figure 2-27 Movement time and AUC, experiment 1



Note. Trials were divided by movement time quintile (<20%, 20-40%, 40-60%, 60-80%, >80%) for each participant, trial difficulty, target side and orientation. Points are the mean movement time for each quintile on the x-axis, and the mean AUC on the y-axis. Horizontal error bars are the within participant se for movement time, and the vertical error bars are the within participant standard error for AUC.

Figure 2-28 Movement time and AUC, experiment 2



Note. Trials were divided by movement time quintile (<20%, 20-40%, 40-60%, 60-80%, >80%) for each participant, trial difficulty, target side and orientation. Points are the mean movement time for each quintile on the x-axis, and the mean AUC on the y-axis. Horizontal error bars are the within-participant standard error for movement time, and the vertical error bars are the within-participant standard error for AUC.

### 2.3.8 Grasp characteristics

The analyses reported above examine the details of reach timing and reach curvature, and how those measures respond to increased choice difficulty. Both experiments also included a manipulation of the orientation of the target and distractor items so that for half the trials the orientation of the non-target was congruent with the orientation of the target. The idea behind this manipulation was to explore whether grasp formation was also influenced by choice difficulty, perhaps via a separate pathway and on a different timescale than the selection of target location.



To calculate hand orientation the data were processed to extract the angle between the line formed by the marker on the knuckle and the ulnar styloid, and the y-axis of the workspace. Appendix C contains graphical analyses of hand orientation in normalised time, which show a lot of individual variation and little consistent difference between easy and difficult choice conditions. As it turned out, it was not clear what measures to extract from these data that could be analysed more formally (analogous to the AUC measure of trajectories). As such, I have not included any analyses of hand orientation in the main body of this dissertation.

## *2.4 Discussion*

The main focus of these studies was to investigate the influence of perceptual difficulty on a rapid reach-to-grasp motion. The hypothesis was that when participants were required identify a target according to a perceptual decision and then reach for it, a difficult perceptual decision may not be fully resolved when the reach is initiated and competition between movement plans will influence the timing and curvature of the executed reach motion. These two studies were intended to develop a paradigm which can be used to investigate how perceptual uncertainty over the choice of reaching target may influence the kinematics of reach-to-grasp actions. The task constrained participants to a two second window to make their judgement and reach and grasp the target object. There were two levels of decision difficulty and two potential locations for the target, with the non-target in the other position. It was also hypothesised that an increase in perceptual difficulty will increase overall reach times, and this hypothesis was confirmed. Also hypothesised was that an increase in choice difficulty will lead to an increase in reach curvature (as measured by AUC) and changes of mind – reaches which initially head towards the incorrect target. These hypotheses were confirmed.

Experiment 1 confirmed the influence of difficulty on reach initiation times, but also revealed that difficulty continued to have an effect once reaches were initiated on both how long the reach movement took, and its curvature towards or away from the non-target. Experiment 1

also showed that reach timing and curvature were highly dependent on both the position of the target on the left or right of the workspace, and whether the target required a grip that was horizontal or vertical, relative to the workspace.

It could reasonably be argued that the influence of difficulty may only be present in relatively few trials where the participant made an initial error in target selection, which participants had the opportunity to correct during the reach. However, the effect of difficulty continued to influence reach timing and reach path even after these “change of mind” trials were removed. Experiment 2 was a modification of experiment 1 with added time pressure on movement initiation. The aim of this manipulation was to increase the incidence of reaches initiated before the decision was fully made. In that way, effects of ongoing competition for target selection may be revealed more clearly.

The addition of the time pressure to the experimental paradigm led to interesting effects that bear further investigation. The effect of difficulty was stable across all measures in both experiments, however pushing participants to move early did increase the incidence of change of mind trials, and also that difficulty still retains an effect on reach path curvature after change of mind trials are removed. This indicates that difficulty changes how reaches are executed even if the reach target chosen with lower information is the correct one.

There were a range of potential result patterns from this experiment, depending on what kind of motor control strategy would be in use by the participants (see Figure 2-1). If the accuracy required of a reach-to-grasp action implies more intensive planning, then participants might have waited until their uncertainty was sufficiently resolved before executing their grasp at any difficulty level. Were that to be the case in this task, there would only have been a significant effect on reach initiation times, with the other measures unaffected. Given that decision difficulty influenced movement time and curvature, the pattern of results clearly contradicts this idea. An extension to this idea – that curvature and movement time will increase because

mistakes in action selection can be revised, would require that any effect of difficulty on curvature will no longer be present once “change of mind” trials are removed. This pattern was also not seen in the data.

Increases in curvature with “change of mind” trials removed, indicate that the effects of increased perceptual choice difficulty are not limited to a simple delay in initiation time reflecting a longer target selection process before an otherwise unchanged reach path. Nor can the increases in reach curvature be explained solely by an increased incidence of changes of mind. The alternative accounts, suggesting either a single initial motor plan to defer the target choice (Wong & Haith, 2017) or that the initial part of the trajectory can be influenced by the incomplete decision (Friedman et al., 2013), are harder to distinguish between with these data. Both suggest that curvatures, as defined by the analysis of the data, would increase with a higher level of perceptual choice difficulty, and indeed this is what the data show.

Of the intermittent control models that are not “pure” change of mind models, one suggestion is that increased curvature will be due to participants selecting a single motor plan directed towards the midpoint between the targets (Haith et al., 2015; Wong & Haith, 2017). This strategy allows participants to start the reaching motion before target selection has finished. Curvature will increase with choice difficulty because there will be a longer period of forward movement before the decision process has finished. However, this explanation also suggests that the time of reach initiation will no longer be informed by the trial difficulty at all, yet even in experiment 2, when there was strong encouragement to move early, more difficult choices led to slower reach initiation. If participants developed a single strategy to defer their choice and make their initial reach uninformed by the stimuli, then reaction times between the easy and difficult choice trials would be quite similar, though there are suggestions that control policy selection (in contrast to target selection) will consume very little of the initial response time (Wong et al., 2015), whereas in these results the average difference between easy and difficult

trials was ~160ms. However, a possible limitation of this analysis is the retention of trials where participants often did not move within the time limit. The final two alternatives are: intermittent control where the initial reach trajectory is either partially informed by the decision process with later refinements (Friedman et al., 2013) or continuous control models where the entire reach trajectory is tightly coupled to the decision process (Lepora & Pezzulo, 2015).

There are some further aspects of the data which also need further examination. It was determined through the analysis that to isolate the experimental effect of choice difficulty it was necessary to include model terms for the target location and orientation, even for initiation time, as well as movement time and curvature. In experiment 1 initiation times to targets on the right were faster, as well as showing an interaction between difficulty and target side when the change of mind trials were removed. This indicates that slower initiation times occurred when the early target selection favoured the left target. It is well established that simple reaction times to targets ipsilateral to the responding hand are faster (Berlucchi et al., 1971), as well as spatial stimulus-response compatibility effects in choice reaction time, where targets on the right area reacted to faster with the right hand than targets on the left (Anzola et al., 1977).

In terms of reach duration and curvature, the consistent differences caused by target side and target orientation need to be explained or accounted for, including the overall negative curvatures for reaches to the right in easy choice trials. Efficient movement of the hand from one position may not be a straight line due to the inertial anisotropy of each joint (Flanagan & Lolley, 2001). For example, it is relatively faster and easier to lift your elbow outwards from your trunk than to push it across your body, and these will require different sequences of muscle contractions (Vandenberghe et al., 2010). It can be seen from the data that the shortest reach duration is for the right-vertical target, with the longest for the left-vertical target, and this is true for both the easy and difficult trials. To reach and grasp a horizontal target on the left (with the right hand) requires simultaneous protraction (forward rotation) of the scapula and

straightening of the elbow joint to move the hand towards the target, and adduction (a clockwise planar rotation) of the wrist so that the index finger is to the front of the thumb for the vertically aligned grip. For a vertical target on the left the grip must be horizontally aligned, requiring the elbow to be held closer to the trunk to accommodate further wrist rotation. To reach and grasp a target on the right, the hand is moved to the target by the shoulder muscles simultaneously abducting and laterally rotating the upper arm away from the body, and either abducting or adducting the wrist for horizontal targets or vertical targets, respectively. This relatively easier initial motion of the arm towards the right could then have led to either ongoing or intermittent control less able to intervene in the ongoing reach process.

The most natural reach-to-grasp action was for horizontal targets on the right, and the most awkward was the vertical targets on the left. Increased movement times may then reflect both a more complex sequence of muscle activations and increased choice uncertainty. Biomechanical influences can also be used to explain why mean reach curvature to rightwards targets was negative overall. Recall that the act of grasping an object requires the hand to approach the target from a direction that will allow the fingers to close perpendicularly on the object (Verheij et al., 2013). This further constraint on the approach vector of the hand towards the object necessarily changes the transport component of the reach, altering the path and increasing the time required for the movement. Overall, the workspace variables of target position and orientation altered the biomechanics of reaching to grasp, but did not consistently interact with the effect of choice difficulty.

## *2.5 Conclusion*

In conclusion, the experiments detailed in this chapter showed that as the difficulty of a perceptual choice increased, movement initiation times increased as well as path curvature and movement time. While biomechanical effects have an influence on reach timing and trajectory, on top of this an increase in the difficulty of choice of reach target strengthens the influence of

decision competition. These hallmarks are not just restricted to increased initiation times alone, which would suggest simply longer processing time for the difficult decisions or restricted to more changes of mind, but show an influence the whole movement in subtler ways which perhaps indicate the co-activation of motor programmes.

Having excluded simpler models which suggest no motor plan mixing, the viable models remaining are those that involve the blending of multiple movement programmes, either intermittently during the task response, or continuously. Given the subtle differences between the predictions of these models, further insights about the interaction between perceptual uncertainty and choice reach-to-grasp actions may be gained with a richer description of the distributions of reach curvature and timing, and this is the aim of Chapter 3.

The experiments and analyses reported in this chapter collected data from many participants, who would each have had an individual level of perceptual skill for the choice stage of the task, and differing levels of joint flexibility, motor skill and limb size, all of which may in turn modify the effect of increasing the difficulty of the perceptual decision on the kinematics of their response. With 96 trials for each subject and a highly variable response both between and within subjects, distributional analyses are impractical. Chapter 3 reports an experiment which attempts to statistically disentangle how curvature distributions will change as competition between movement targets increases on an individual basis. Will the subtle effects detected from experiments 1 and 2 manifest themselves in shifts in the location, scale, or skew of these distributions? Answering this type of question will require careful analyses of the distributions. Therefore, the study reported in Chapter 3 involved only five participants performing many trials over multiple sessions. These distributions will then be used later to inform an investigation of the continuous flow model of Lepora and Pezzulo (2015). This investigation is reported in Chapter 4. This model assumes a continuous link between the decision variable and the reach target, via a weighted combination of motor plans. The question is whether this model can

account for the distributional changes induced by increased perceptual uncertainty.

Furthermore, insight into the influences of biomechanical constraints of both grip approach and the asymmetrical inertia of upper arm movements on reach curvature distributions will be disentangled from decision components with the addition of a non-decision baseline condition.

## Chapter 3 The curvature of reach-to-grasp trajectories launched during perceptual choice emerge from separable processes

Chapter 3 reports a replication and extension of experiment 2 from Chapter 2. Through the collection of many more trials and the addition of a baseline condition, the experiment aimed to estimate and separate the contributions of decision processes from those introduced by motor variability and biomechanical factors. As well as broadly replicating the LMM analyses from chapter two, the distributional analysis tested whether a shift in one or all of the baseline parameters was sufficient to parsimoniously explain the empirical curvature distributions collected under choice conditions. Rather than a change to the baseline distribution, the best fit for most choice distributions was a weighted mixture of the baseline distribution with an additional ex-Gaussian distribution. These results are discussed in the context of the likely features of a model which can simulate a link between an evidence accumulation process of decision making to reach paths executed under conditions of increased perceptual uncertainty.



### 3.1 *Introduction*

The overall aim of this thesis is to explore how perceptual uncertainty influences movement in a naturalistic reach-to-grasp action, and whether a process which links ongoing decision making and reach path generation can be modelled. The experiments reported in Chapter 2 allowed for some initial insights into how temporal and spatial aspects of the reach-to-grasp movement were influenced by both perceptual choice difficulty and the position and orientation of the targets. Overall, increased difficulty increased initiation time, movement duration and, therefore, the overall time to get the hand onto the target.

Trajectory curvature was assessed using an Area Under Curve (AUC) measure. AUCs were calculated as the (signed) area between the actual trajectory traced by the hand on its path to the target and the direct line between the starting and terminal position of the hand. On average, these areas were more positive in the hard-choice condition, suggesting attraction to the non-target. Removing changes of mind from the analysis did not eliminate the effect of choice difficulty from curvature. Both temporal and spatial parameters were affected by a number of basic “workspace” effects (e.g. target side), sometimes in interaction with choice difficulty. However, as each participant completed relatively few trials, all of which involved some element of choice, effects on timing and curvature not due to decision processing (e.g. workspace and biomechanical constraints) were difficult to disentangle from any effects introduced by increased choice difficulty. In addition to this each participant was required to adapt to a fairly novel experimental task, so that we may not be able to detect whether the effects of interest survive once the participant has become very familiar with what was required of them. It is clear that most tasks requiring large and or rapid movements in three dimensions have abundant degrees of freedom permitted by the three-dimensional response space, as well as a large degree of inherent variability due to motor noise. Therefore, it is conceivable that participants may settle on a relatively limited number of motor programmes (determined by the

workspace and target orientations). They may learn to select the most appropriate movement rapidly, thereby eliminating any influences from the decision process on the evolving reaching movement.

Based upon the findings from chapter one, it appears that an increase in choice difficulty increases reach curvature due to effects from competition between parallel motor plans, rather than a mixture of sequential, single movements. Recall that single motor plan models suggest that under conditions of target uncertainty, participants will execute a reach towards an intermediate location, to be corrected in-flight once a decision can be made. Were this to be a consistent strategy, we would not expect an effect of target difficulty to impact overall initiation times. Studies which find this behaviour are usually ones in which the target location can only be known after reach initiation, so may be more accurately be termed experiments into the effect of target ignorance, rather than situations in which target certainty is dynamically resolving. The simple “change of mind” model, on the other hand, would predict no influence of trial difficulty at all once such trials are removed from the analysis. What is left are the models which suggest that reach path curvatures are indeed due to competition between alternative movement plans at reach onset, either continuously (Lepora & Pezzulo, 2015) or under intermittent control (Friedman et al., 2013). For this extension to naturalistic reach-to-grasp actions, the curvature from motor plan competition comes on top of any natural curvature given the target position and orientation.

The experiment reported in this chapter was a replication and extension of experiment 2.

Collecting data from fewer participants, but with many more trials, allows for a much more in-depth analysis of the distribution of curvatures in each difficulty condition. Moreover, the inclusion of single-target baseline trials without a choice allows for an examination of non-decisional influences on the trajectories. With this approach, the variability in trajectories solely due to workspace or biomechanical constraints and internal motor noise may be estimated. The

effect of the imposition of a choice process on the reach-to-grasp action may then be more closely studied. Finally, armed with more reliable distributions of trajectory curvature at the level of individual participants, I can compare these distributions to the predictions from the computational model of Lepora and Pezzulo (2015). This comparison is reported in Chapter 4.

We know from the Chapter 2 that when the difficulty of the perceptual choice is increased there is an increase in the mean curvature as well as an increase in the variability of that curvature.

Without the need to make any perceptual decision, a participant has only to locate the target, generate a single action plan, and then launch the movement. Given that we expect some variability in this process, we can ask whether the addition of choice merely modifies this process, or whether having to make a perceptual decision requires a more radical change. To examine how adding a perceptual decision changes the reach-to-grasp action we can compare curvature distribution between the baseline and the choice conditions.

It is important to note that this approach allows a comparison of two alternative explanations for why curvature is observed to increase in the higher difficulty condition when compared to the baseline trials or the easy condition. In both explanations it is accepted that the resolution of a decision-making process will take some time, and that reaches launched before the decision is made are based on incomplete information about which is the proper target.

The first explanation is that the ongoing dynamics of decision-making influences all reach paths to some degree because reach planning and decision making are heavily intertwined. If, at launch, the decision between targets is unresolved a blended representation of the reach action is used, and curvature will arise from the ongoing decision process resolving the reach plan itself. In this scheme reaches which are launched towards the incorrect target will be those where the decision (at launch) favours more the incorrect target, while reaches launched towards the middle will be those where the decision process is equivocal about the target and reaches towards the correct target will be those where the decision process favours the correct target at

the moment of launch. At an individual trial level increased curvature in the difficult choice condition occurs because slower decisions lead to more of the reach proceeding towards a blend of targets. At the level of the distribution of curvatures, the addition of choice processes will change all reach paths and the distribution of curvature values calculated from them will be a modification of the baseline distribution in some way, either as an overall shift or a stretch of the baseline distribution.

The second explanation is that decision-making and reach planning are more separate than implied above. If a reach is launched without time for the decision process to resolve, the initial direction of the launch will be to either the correct target or the incorrect target. There is no blending of reach plans, so increased curvature during more difficult decision-making is just from lower accuracy in the choice of initial reach direction. If the initial reach direction is correct, then the reach path under choice will be generated using the same information as in the baseline condition. Here there will be a set of curvatures which follow the same distribution as the baseline reaches, with an additional component which does not resemble the baseline distribution.

In summary, the distributional analysis will be able to determine which of the above explanations are more likely to lead to the shift in curvature distributions. Should there be a continuous link between decision processes and ongoing actions, we may expect that all reaches will be influenced by the presence of a distractor and the need to make a choice. Since all choice reaches may experience some “attraction” to the distractor, the entire distribution of trajectory curvatures will be moved in a positive direction. When the perceptual decision is difficult to resolve quickly this influence will be stronger, but of the same kind. Alternatively, the imposition of choice on the process may exert a more subtle effect, perhaps just increasing the curvature for a small number of reaches, thereby increasing just the right-hand tail of the distribution. Finally, it is possible that the addition of choice generates a separate population of trajectories

(e.g. changes of mind), suggestive of a separate or additional mechanism. These different possibilities may be examined with more detailed analyses of the distributions of curvature at the level of individual participants. The primary aim of this chapter is to conduct this analysis.

## 3.2 *Method*

### 3.2.1 Participants

Five right-handed participants, all female, each attended five one-hour sessions for which they received a fee. Ethical clearance was obtained from the local Faculty of Science Human Research Ethics Committee. All participants provided written informed consent and were fully debriefed.

### 3.2.2 Design

In a fully repeated measures design, each participant attended five sessions on consecutive days, at the same time of day. Across the five sessions thirty experimental blocks of twenty trials were recorded, totalling 600, with six blocks in each session, totalling 120 trials. Similar to experiments 1 and 2, four independent variables were manipulated: (i) Difficulty, (ii) Target Side, (iii) Target Orientation and (iv) Distractor Orientation. In addition, there was a baseline condition in which only one target was placed on the workspace, on either the left or right, and in a vertical or horizontal orientation. As before the instruction for each block was to pick up the lighter or darker target. In the baseline condition there is no competitor target. Within each block of twenty trials there were eight easy trials, eight difficult trials and four baseline trials, in a randomised order.

### 3.2.3 Materials

As with experiments 1 and 2, two pairs of grey blocks were used as stimuli (easy choice-difficulty pair, 22.3 cd/m<sup>2</sup>, 56.7 cd/m<sup>2</sup>; hard choice-difficulty pair, 30.0 cd/m<sup>2</sup>, 42.3 cd/m<sup>2</sup>), with the single target for the baseline trials being the same object used for the practice trials (41.1 cd/m<sup>2</sup>). The placement for the blocks was 20cm forward of the start position, and 30cm each side of the

participant's midline. The same spring button and plate was positioned under the start position to record approximate launch times and provide feedback if the participants did not initiate their reach within 400ms of the trial start. Customised MATLAB code triggered the occlusion screen, sent timing events and trial information to the motion capture system, and recorded launch times and provided audio feedback to the participant if they had not initiated their reach before the time limit.

### 3.2.4 Procedure

The motion capture space was calibrated before each session. Similar to experiment 2, for each session participants sat in a position where they were able to see the targets through the occlusion screen and also comfortably reach the targets. Reflective markers were placed on the right (dominant) hand. Four practice trials were completed at the start of the session, and these were followed by the six experimental blocks. Between each trial the screen occluded participants' vision of the workspace while the experimenter arranged the target or targets according to a randomised order. Before each trial the participants were reminded which target (bright or dark) they were to reach for, whether or not there was a competitor target (on choice trials) or not (on baseline trials).

### 3.2.5 Data Processing

#### *3.2.5.1 Analysis Pipeline – Raw and Exported Data*

Raw motion capture data was processed in a procedure identical to experiments 1 and 2. The labelled and exported data was processed using the same customized MATLAB code, modified only to account for the presence of a baseline condition in the experiment.

In terms of trial exclusion, only four trials were removed due to motion tracking errors, all from the baseline condition. In experiments 1 and 2 trials were also excluded for taking over two seconds to complete, however none of the trials recorded in this experiment fit that criterion.

Overall reach errors were also rate with 18 trials from the easy choice condition and 58 trials from the hard choice condition not subject to further analysis.

### 3.2.6 Statistical Analysis

First, I assessed to what extent the results from chapter 2 replicate, by analysing the data from just the choice conditions. The same mixed-effects model was used as in Chapter 2. Although this statistical assessment was not the primary aim of this chapter, it was useful to see how the effects reported in Chapter 2 would fare once participants are tested much more extensively.

Second, I then report an in-depth analysis of the distribution of curvatures at the level of individual participants. A visual examination of the distributions in the no-choice baseline condition suggested that an ex-Gaussian distribution may be a suitable parametric form to describe the variability in the trajectories. The ex-Gaussian is the sum of a Gaussian and exponentially distributed random variable. It generates a distributional shape that can vary from symmetric and Gaussian (i.e. a small contribution of the exponential component) to strongly skewed with a heavy right-hand tail (i.e. a large contribution of the exponential component). The ex-Gaussian is frequently used to model data that exhibit strong right-hand skew, like reaction times and, as it turns out, the AUC measure of trajectory curvature adopted here. The logic was to fit this distribution to each participant's baseline AUCs (separately for left and right). We then assess what needs to change in this distribution in order to accommodate the AUCs in the choice conditions. Both the linear mixed effect models and the curvature distribution models will be assessed using the AIC.

## 3.3 *Results*

In this section I will first report a qualitative assessment of reach trajectories. After this, a replication of the statistical analysis approach in Chapter 2 on reach timing and curvature is carried out, using all the data collected for the choice condition trials. Next, a model fitting

approach is taken to assess how the distribution of curvatures in the baseline, no choice, condition could be modified to account for the distribution of curvatures in the choice conditions. An explanation of the model fitting approach is presented with representative data from one participant, before fit parameters for all participants are assessed.

### 3.3.1 Reach path differences

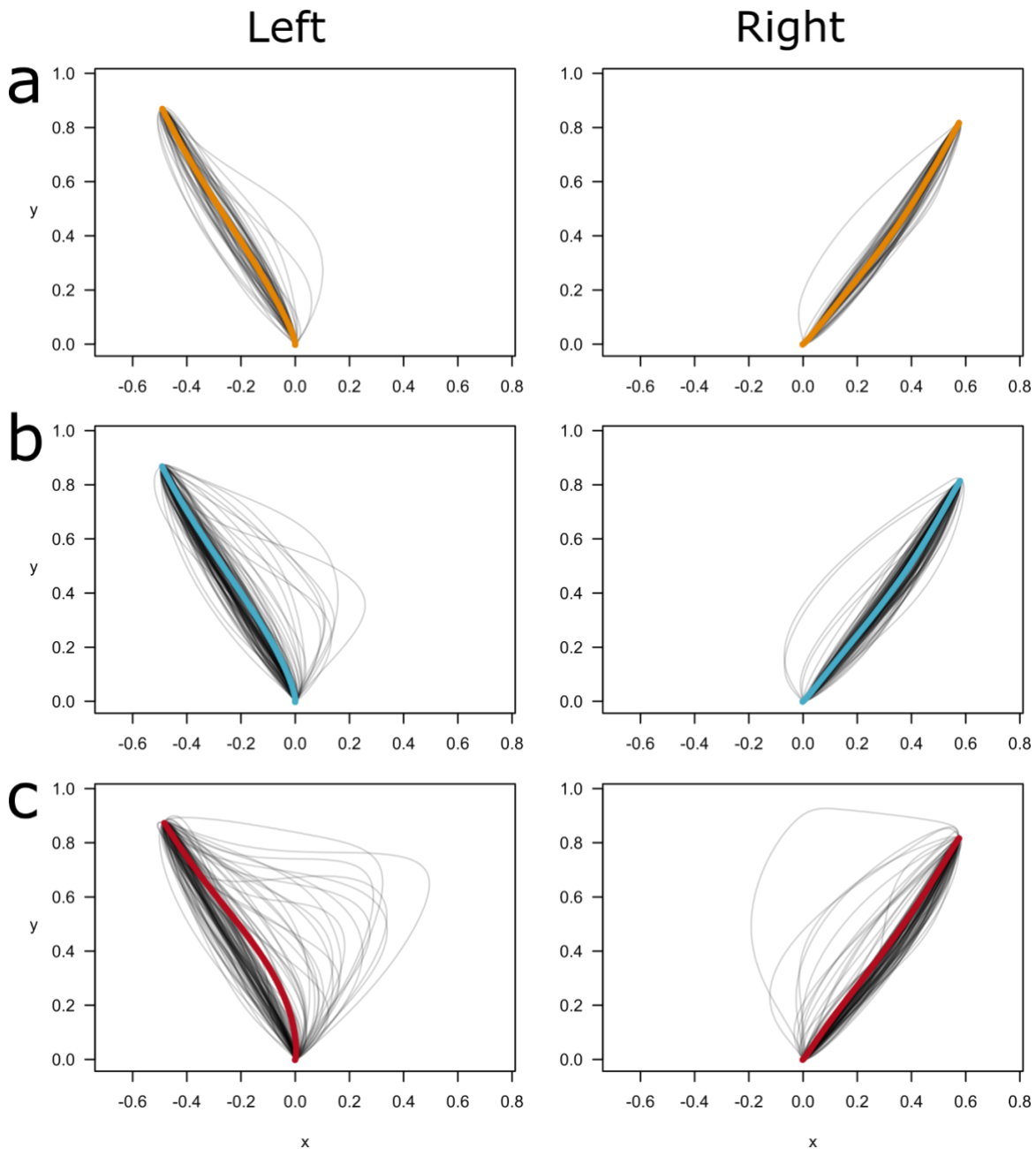
Figure 3-1 shows all the trials recorded for participant 4 in which they picked up the correct target, separated by choice and difficulty condition and target side, along with the average trajectory for each condition. The mean path is calculated by first scaling the reach extent to a unit distance so that the straight line between the start and end position is of length 1, then resampled using a cubic spline at 101 equally spaced time points and separately averaging the x-coordinates and y-coordinates for all reaches in that condition. In each plot the end points of each reach are then aligned with the endpoint of the mean trajectory. In comparison to the baseline and easy choice condition, the incidence of trials in which there is a large deviation away from the stereotypical reach increases when the perceptual choice is difficult. Notably there are a few trials even in the baseline condition where the participant did not take the direct route to the target, a pattern seen in all participants except for participant five (see Appendix B for the same information for the remaining participants).

Several preliminary insights can be gleaned from this visualisation. Low curvature is seen in many trials, even in the hard choice condition, and do not seem to show any conflict at all. Measures of mean curvature will be primarily influenced by these low curvature trials, with only a minority of trials with large curvature contributing to a mean shift between experimental conditions. Visual inspection of the individual trial data in Figure 3-1, particularly the hard choice condition for left side target retrievals shows a variety of possible trajectory types. Trajectories with a strong influence on mean curvature may be reaches that either initially go to the non-target, or an intermediate direction to neither target, before curving towards the participants'



ultimate choice. Furthermore, of the trajectories with an obviously higher curvature than the mean reach path, some may be reflecting different strategies. In the hard choice condition

Figure 3-1 Participant 4 mean reach trajectories and individual trial paths

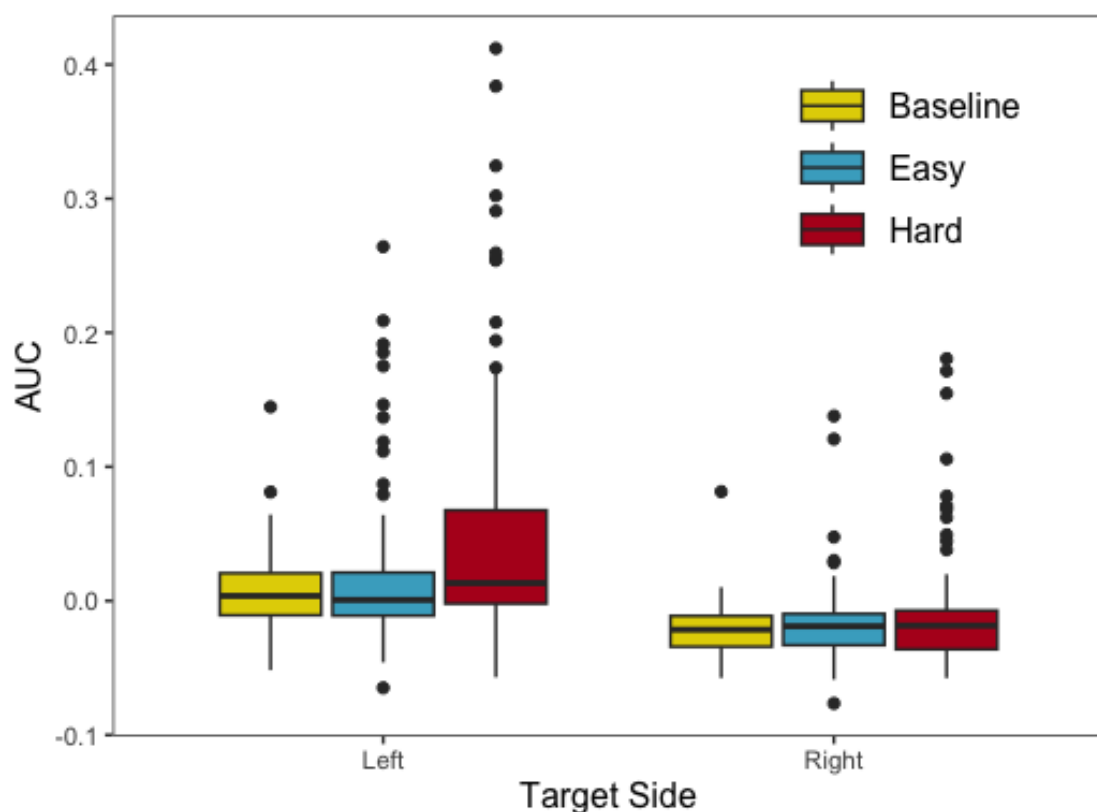


Note. Each panel shows all successful trials recorded for participant 4 in grey, with the mean path overlaid. Panel rows are (a) Baseline no-choice trials, (b) easy choice trials and (c) hard choice trials. Left panels are reaches to left targets, and right panels are reaches to right targets. For each reach the start point and end point are aligned.

reaches to right side targets there are two trajectories that begin travelling to the non-target before a revision of movement, and two which head forwards from the start point before

curving towards the target. Notable, too, is the clear difference in incidence of larger curvature trials for left targets than for right targets in both the choice conditions, with many more “change of mind” trials visible in left target reaches. Figure 3-2 presents boxplots of the AUC values recorded for participant 4. The location of the does not shift greatly between the easy choice condition and the hard choice condition, however it does appear to be stretched upwards for both sides as difficulty increases. Thus, reliance on mean summary measures collapsed across all trials in a single difficulty or target side condition may be misleading for data like these. This result underscores the importance of more detailed analysis of the distributions of AUC values.

Figure 3-2 Distribution of AUCs for participant 4



Note. Boxplot of the AUC values for the reaches of participant 4. Reaches in the baseline condition, the easy choice condition and the hard choice condition are presented, and split across reaches to targets on the left and the right.

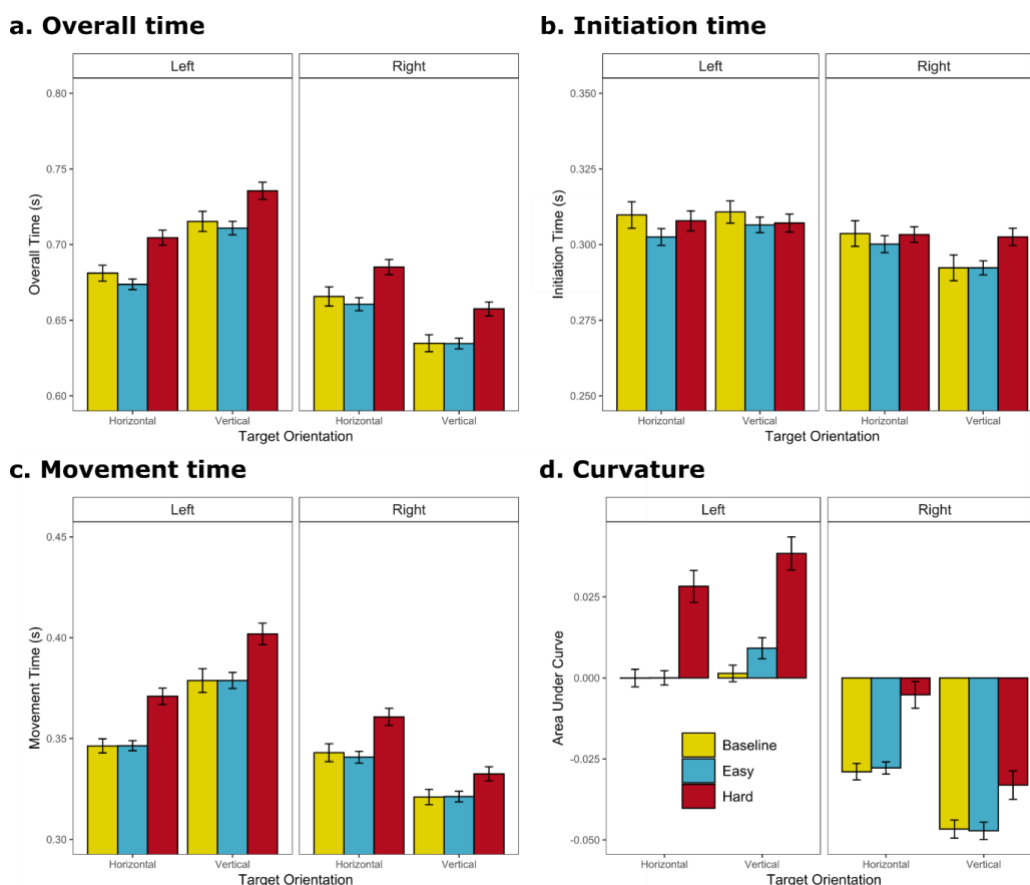
A notable difference between left and right reaches is that the *range* of AUC values is greater for reaches to targets on the left, than to targets on the right. This pattern is also seen in the

boxplots of AUCs for the other participants (see 0, Figure 0-6 to Figure 0-10). The median curvature values are more similar, and the reader is directed to Figure 0-11 in the Appendices for this comparison.

### 3.3.2 Average reach timing and curvature measures

An assessment of the timing and curvature differences between all conditions, pooled across participants, is presented in Figure 3-3. In terms of the reach timing, a similar pattern of data is seen as in experiment two. Overall reach times are, on average, higher for the hard choice condition than the easy choice or baseline trials. Between the baseline, no-choice trials, and the

Figure 3-3 Timing and curvature measurements for all data



Note. Error bars represent within participant standard error. Panel a is the overall time of reach actions – from the start of the trial to the grasp. Panel b is the initiation time – from the start of the trial to the initiation of movement. Panel c is movement time – from the initiation of the reach action to the grasp. Panel d is the curvature, calculated as the signed AUC, as detailed in Chapter 2. Bars are grouped according to the orientation of the target, and plots are split according to the side of the target.

easy choice trials there is a visual trend for increased reach times in the baseline condition. A linear mixed model analysis (reported in Appendix B, Table 0-1) was used to explore whether there was a difference between Easy condition trials and the Baseline condition trials, and the Easy condition trials and the Hard condition trials. All parameter estimates which reflected the Baseline-Easy difference were not significantly different from zero.

### 3.3.3 Linear mixed model analyses

It is important to establish whether and to what extent the results from experiment 2 replicate in the current setting where we have fewer participants do many more trials, including baseline trials. That is, it is possible that more extended training and the inclusion of baseline trials, may abolish some of the effects shown in Chapter 2 or, indeed, reveal novel effects. Therefore, the baseline trials did not include a distractor target the data from the choice trials only were subjected to the same mixed-effects analysis as performed on the data from Chapter 2. Of the remaining choice trials, the number and percentage of incorrect target reaches removed for the statistical analysis are detailed in Table 3-1.

Table 3-1 Number and percentage of trials of incorrect reach actions for each participant

Choice	P1	P2	P3	P4	P5	Total
Easy	6 (2.5%)	2 (0.8%)	4 (1.66%)	2 (0.8%)	4 (1.6%)	18 (1.5%)
Hard	20 (8.3%)	7 (2.9%)	6 (2.5%)	16 (6.6%)	9 (3.8%)	58 (4.8%)

Note. Table lists the number of wholly incorrect reach actions (out of 240 easy choice trials and 240 hard choice trials in the experimental paradigm for experiment 3). Figures in parentheses are the percentage of total trials each participant completed in each difficulty condition.

As before, the data were entered into LMM with participant as a random intercept, and choice difficulty (easy or hard), target side (left or right), target orientation (horizontal or vertical) and distractor congruency (congruent or incongruent) as fixed effects, along with all potential interactions between those fixed effects. Without the baseline trials the effect estimate for difficulty is between the easy choice condition and the hard choice condition. These results are presented in Table 3-2.

The overall time taken for each reach-to-grasp increased in the higher difficulty condition, for leftward reaches and for vertical targets, as can be also seen in Figure 3-3, above. As in the data from experiments 1 and 2, there is an interaction between target side and target orientation. In the final model for initiation time only target side and trial difficulty remain as significant effects after backwards selection. Initiation time was slower for hard-choice trials, and faster for reaches to the right. For movement time we see a similar pattern of data as for overall time, with difficulty, target side, target orientation and the interaction between side and orientation exerting an influence on movement time.

Table 3-2 Regression coefficients and standard errors for main effects and interactions for experiment 3 (comparing Easy and Hard difficulty trials)

Term	Overall Time (inverse)	Initiation Time (inverse)	Movement Time (inverse)	AUC (untransformed)
Random Effects:				
Participant Variance	0.14	0.44	0.34	0.017
Residual Variance	0.14	0.48	0.37	0.056
Fixed Effects:				
(Intercept)	-1.497 (0.061) ***	-3.4 (0.2) ***	-2.93 (0.15) ***	-0.0069 (0.0078)
Difficulty	0.0223 (0.0028) ***	0.0209 (0.0099) *	0.0528 (0.0078) ***	0.0098 (0.0012) ***
Target Side	-0.0526 (0.0028) ***	-0.0284 (0.0099) **	-0.1458 (0.0078) ***	-0.0255 (0.0012) ***
Target Orientation	-0.00083 (0.00283)	.	-0.0035 (0.0078)	0.0037 (0.0012) **
Side x Orientation	0.0307 (0.0028) ***	.	0.0984 (0.0078) ***	0.0085 (0.0012) ***
Difficulty x Side	.	.	.	-0.0041 (0.0012) ***
Full Model AIC	-2449.3	3286.5	2192.4	-6536.5
Final Model AIC	-2572.7	3178.9	2093.5	-6658.7

Note. Table shows the fixed effect and random effect parameters for overall time, initiation time, movement time and AUC for correct trials in the choice conditions from experiment 3 after a backwards selection procedure from a fully interacting model. A negative reciprocal transform has been applied to the timing measures. The parameter estimates are shown with their respective standard error in parentheses.

Significance codes: \*\*\*  $p < 0.001$ , \*\*  $p < 0.01$ , \*  $p < 0.05$ , †  $p < 0.1$

The pattern of results for the curvature metric are similarly driven by choice difficulty and target placement (side, orientation, and their interaction), with an extra effect attributed to the interaction between difficulty and target side. This interaction indicates a lower difference in mean AUC between easy-choice trials and hard-choice trials for targets on the right, than for targets on the left.

As in chapter 2, the same statistical analysis process can be applied after removing trials in which we can identify a potential “change of mind”. The procedure to make this identification is to detect a peak in the x-axis (left to right) movement of the knuckle marker which marks a turning point between movement towards the distractor target and movement towards the correct target. The number and percentage of “change of mind” trials for each participant and in each condition are detailed in Table 3-3. As suggested by visual inspection of the trajectories in Figure 3-1, more change of mind trials occurred in the hard choice condition.

Table 3-3 Number and percentage of change of mind trials for each participant in each choice condition

Choice	P1	P2	P3	P4	P5	Total
Easy	70 (29.2%)	35 (14.6%)	23 (9.59%)	30 (12.5%)	7 (2.92%)	165 (13.8%)
Hard	82 (34.2%)	77 (32.1%)	47 (19.6%)	55 (22.9%)	25 (10.4%)	286 (23.8%)

Note. Each cell reports the count of “change of mind” trials for each participant in the difficulty conditions of Easy and Hard reaches. The percentage value is the proportion of change of mind trials relative to all trials where the correct target was grasped.

Again, a backwards elimination procedure was applied to the full model, which included every potential factor and all interactions with terms which did not contribute to model fit dropped sequentially. These results are displayed in Table 3-4.

Table 3-4 Regression coefficients and standard errors for main effects and interactions for experiment 3, with change of mind trials removed

Term	Overall Time (inverse)	Initiation Time (inverse)	Movement Time (inverse)	AUC (untransformed)
Random Effects:				
Participants Variance	0.13	0.41	0.33	0.017
Residual Variance	0.13	0.45	0.34	0.023
Fixed Effects:				
(Intercept)	-1.51 (0.06) ***	-3.36 (0.18) ***	-3.02 (0.15) ***	-0.0295 (0.0076) ***
Difficulty	0.0138 (0.0032) ***	0.034 (0.012) **	0.0175 (0.0085) *	0.00132 (0.00059) *
Target Side	-0.0462 (0.0036) ***	-0.089 (0.013) ***	-0.1005 (0.0093) ***	-0.01044 (0.00065) ***
Target Orientation	0.00089 (0.00344)	-0.0047 (0.0121)	0.009 (0.009)	0.00297 (0.00062) ***
Side x Orientation	0.0304 (0.0034) ***	0.033 (0.012) **	0.091 (0.009) ***	0.00872 (0.00062) ***
Distractor Congruency	.	9.1e-05 (1.2e-02)	.	-0.00085 (0.00062)
Difficulty x Side	.	0.005 (0.012)	.	.
Difficulty x Distractor Congruency	.	0.012 (0.012)	.	.
Side x Distractor Congruency	.	0.0056 (0.0121)	.	0.00068 (0.00062)
Difficulty x Side x Congruency	.	-0.024 (0.012) *	.	.
Orientation x Congruency	.	.	.	0.00101 (0.00062)
Side x Orientation x Congruency	.	.	.	-0.00158 (0.00062) *
Full Model AIC	-1793.6	2148.7	1207.1	-7159.0
Final Model AIC	-1913.8	2097.1	1104.7	-7256.6

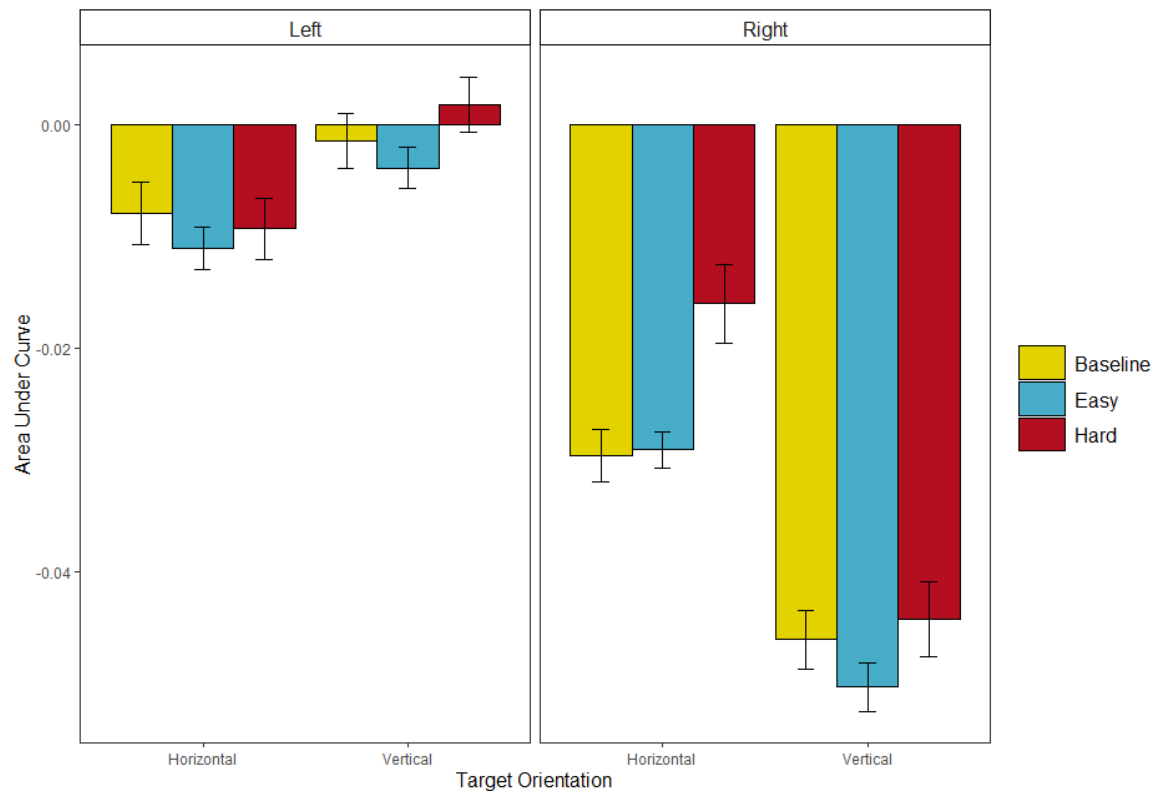
Note. Table shows the fixed effect and random effect parameters for overall time, initiation time, movement time and AUC for correct trials in the choice conditions from experiment 3 after a backwards selection procedure from a fully interacting model. A negative reciprocal transform has been applied to the timing measures. The parameter estimates are shown with their respective standard error in parentheses.

Significance codes: \*\*\*  $p < 0.001$ , \*\*  $p < 0.01$ , \*  $p < 0.05$ , †  $p < 0.1$ , ns not significant.

With regards to reach timing, the effects identified for overall time and movement time are similar to those of the statistical model which included changes of mind, wherein difficulty, target side, and the interaction between target side and target orientation had a significant effect on these measures. However, this consistency breaks down for initiation time, where the effect of difficulty is strengthened and also shows up in interaction with target side and distractor congruency. For curvature, the backwards elimination procedure retained an interaction between target side, target orientation and distractor congruency, however this does not include an interaction with difficulty. As such, we can conclude from this analyses that the processing of the perceptual choice is indeed having an effect on reach-path curvature, but this separate to any influence from the placement of targets in the workspace. As can be seen in Figure 3-4, removal of change of mind trials appears to have nearly eliminated the large effect of

difficulty on left-ward reach path curvature. Recall from Figure 3-1 that such extreme trajectory deviations occurred more often for leftward targets, and this effect may be observed in the path traces for all five participants (see 0, Figure 0-1 to Figure 0-5).

Figure 3-4 Average curvature values for experiment 3 with changes of mind removed



Note. Mean AUC values summarised over all participants and separated into left and right reaches, and horizontal and vertical target orientations, with change of mind trials removed from the analysis. Error bars represent within-participant standard error.

The change in mean curvature for the hard-choice condition when changes of mind are removed may be due to both a preference for right side targets (by the right-handed participants) and the way that changes of mind are identified. A bias or preference for initiating movements to targets on the right can be seen in the consistently lower mean initiation times. The lower overall movement time for rightwards reaches tells us that the movement itself is also easier to execute. As can be seen visually on the trajectory plots (Figure 3-1) there seems to be a greater incidence of large curvature reach paths when targets are on the left. This may be caused by a lower response initiation threshold for targets on the right. The fallout of this would naturally be lowered initiation times, shorter movement times (when this is the correct choice) and more

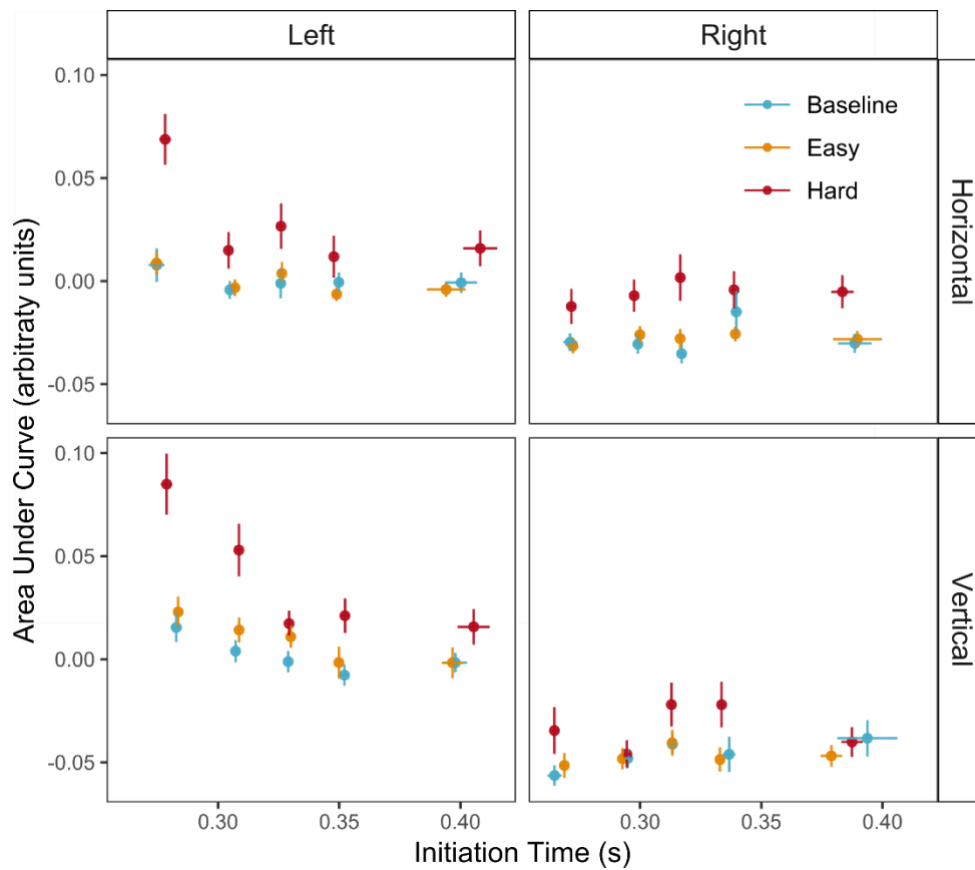


erroneous launches which need to be corrected. However, it must be acknowledged that changes of mind are identified by examining the path that the knuckle takes, and this may be influenced by biomechanical constraints. If this path includes a section where there is a reversal in the x-direction (as outlined in Chapter 2), and this reversal is contralateral to the grasped object, a change of mind is flagged. When lifting the hand, a small deviation to the right side of the workspace is often seen, however making an *a priori* judgement about which deviations are solely due to the mechanics of arm reaching, and which may be due to possible changes of mind coincident with reach initiation may introduce researcher bias into this calculation.

#### *3.3.3.1 A bias in initial reach direction*

Below, Figure 3-5 shows the mean AUC values from experiment 3 conditioned on initiation time quintile. For reaches to left targets, reaches initiated earlier show much greater curvature toward the non-target, with this difference diminishing at longer initiation times, but not disappearing. This pattern is less apparent for reaches to right targets, though there is usually an increase in curvature for hard-choice trials.

Figure 3-5 Curvature vs initiation time for all successful reaches in experiment 3



Note. Each panel shows the mean curvature conditioned on initiation time quintile (<20<sup>th</sup>, 20<sup>th</sup> – 40<sup>th</sup>, 40<sup>th</sup> – 60<sup>th</sup>, 60<sup>th</sup> – 80<sup>th</sup>, and >80<sup>th</sup>) from all participants in experiment 3. The horizontal error bars represent the within-participant standard error of the mean initiation time within each quintile for each participant, and vertical error bars the within-participant standard error for mean AUCs. The points are coloured according to the trial difficulty condition.

The larger and more variable AUCs for reaches to the left in the hard-choice condition may then be due to a set of trials where participants chose to initiate their reaches rapidly, and mostly to the right target, before the correct target had been identified. In trials where the target was on the right side there would not be a need for a corrective action, but when targets are on the left, a corrective action will have been needed to ensure trial success. For the baseline and easy-choice reaches, this correction may have occurred very early with little impact on AUC, but for the hard-choice trials, the correction will have occurred later, and led to more trials with a large AUC value.

The tendency to make a “default” reach to the right at low initiation times can be examined further by looking at the correspondence between these initial reaches, divided again by the

initiation time quintile. We can further break down initial reach direction by including the target side for the current trial. As can be seen in Table 3-5 there is a strong tendency for an initial reach to the right (488 to 112 leftward reaches in quintile 1, collapsed across target side). Only for the slower reaches to the left target (quintiles 4 and 5) are more than half initial reaches towards the correct target. For reaches to targets on the right, the proportion of initial reaches which are to the incorrect target is relatively stable at around 8%.

Table 3-5 The direction of initial reaches, conditioned on initiation time quintile and target side

Target Side	Initial Reach	Initiation time quintile					Overall
		1	2	3	4	5	
Left	Left Initial	89 (29.7%)	126 (42%)	145 (48.3%)	156 (52.2%)	181 (60.5%)	697 (46.5%)
	Right Initial	211 (70.3%)	174 (58%)	155 (51.7%)	143 (47.8%)	118 (39.5%)	801 (53.5%)
Right	Left Initial	23 (7.7%)	30 (10%)	19 (6.3%)	27 (9%)	21 (7.1%)	120 (8%)
	Right Initial	277 (92.3%)	270 (90%)	281 (93.7%)	272 (91%)	274 (92.9%)	1374 (92%)

Note. Target Side is the side of the workspace that the correct target was on. Initial Reach is the direction that the participant reached towards. Initiation time quintile was calculated by ordering all reaches according to the initiation time.

To explore the effects of target side and initiation time on initial reach direction, the entire data set was analysed using a mixed effects logistic regression using *glmer* from the *lme4* package (Bates et al., 2021) to predict whether the initial reach direction on a trial was to the right or the left. Each participant was assigned a random intercept, and we investigated the following set of fixed effects by successively introducing them in models of increasing complexity: Target side (left or right), initiation time, trial difficulty (baseline, easy or hard) and the target side on the previous trial. The model comparison is reported in Table 3-6, and there is a disagreement between the AIC and BIC values for the best model. AIC highlights the most complex model as the best fit to the data – the direction of an initial reach depends on the current target side, the initiation time of the reach, the trial difficulty and the location of the target on the previous trial. However, the BIC value highlights a simpler model which just includes the initiation time of the reach and the current target side and the interaction between them. From this analysis we may

be confident that the pattern of results in Table 3-5 is reliable, and that there may be smaller effects of trial difficulty and previous target location.

Table 3-6 Model comparison of mixed effects logistic regression

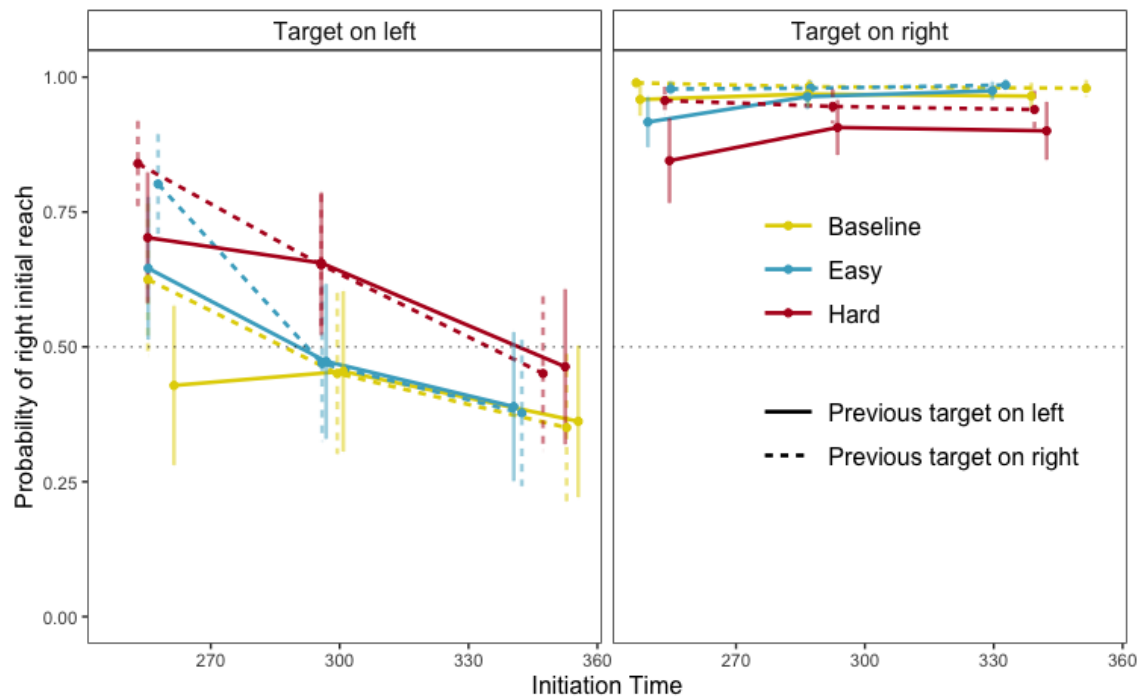
	Model	Free parameters	AIC	BIC
1	Random intercepts only model.	2	3176.5	3188.5
2	Random intercepts + Current target side	3	2491.6	2509.7
3	Model 2, plus initiation time (continuous) and target side interaction	5	2417.1	<b>2447.1</b>
4	Model 3, plus trial difficulty, interacting with target side and initiation time	13	2379.2	2457.2
5	Model 4, plus previous trial target side and the interaction with all other fixed factors	25	<b>2360.6</b>	2510.7

Note. AIC and BIC values are displayed for each model. Models were fit using a binomial mixed effects model with a logistic link function, and parameters were estimated using Maximum Likelihood. The best fitting model according to AIC was the full model with all interactions, while the best fitting model according to BIC was the one with just the current target side and the initiation time as fixed factors.

To help visualise the results of the logistic regression,

Figure 3-6 shows the probability of making a reach to the right when the trial target was either on the left or the right, whether the trial difficulty was a baseline no-choice trial, an easy-choice trial or a hard-choice trial, and whether the previous trial target was on the left or the right, and further divided into early, middle and late trials. For the purpose of the visualisation estimates were calculated from a version of Model 5 but with the initiation time binned into three categories: the fastest third of initiation times, the middle third of initiation times, and the slowest third of initiation times. We can see from the figure that there is an overall bias to initially reach to the right-hand side, even for targets on the left, but this bias is reduced at slower initiation times. Furthermore, at fast initiation times there is a bias towards the location of the target on the previous trial.

Figure 3-6 Probability of an initial reach to the right



Note. Plot shows the probability of an initial reach to the right hand side of the workspace, conditional on the actual target side (left panel for targets on the left, right panel for targets on the right), the initiation time of the reach (divided equally into three bins for early reaches, middle reaches, and late reaches, with points aligned at the average initiation time for each bin), the difficulty of the trial, and whether or not the previous target was on the left or the right. The dotted line at 0.5 represents the point at which an initial reach to the left or right is equally likely, and the error bars is the standard error of the response probability, which was back transformed from the logit scale.

This pattern of initial reach directions can be used to explain the greater variability in AUC for reaches to the left target and the occasional baseline trial which goes in the wrong direction. The overall bias for making an initial rightwards reach can be explained as the participants defaulting to the reach direction which required the least biomechanical effort, which for these right-handed participants was a reach to the right. Initial mistakes in baseline trials are similarly driven by the tendency to default to the right, with the occasional mistake to the left (on a right-target trial) occurring fractionally more often if the previous target was on the left.

### 3.3.4 Distributional Analysis

This section presents a more in-depth analysis of the distribution of curvatures. The data for participant 4 is worked through to demonstrate the process. A pair of probability distributions

for reaches to the left and right should capture most of the variability inherent in reach paths originating from non-decision influences. These non-decision influences include effects of target side, any biomechanical constraints which limit the smoothness and latency of muscular activation, and motor noise introducing both inaccuracies in launch trajectory and any associated need for small late-reach corrective movements. Reaches towards horizontal and vertical targets were combined to improve the stability of parameter optimisation.

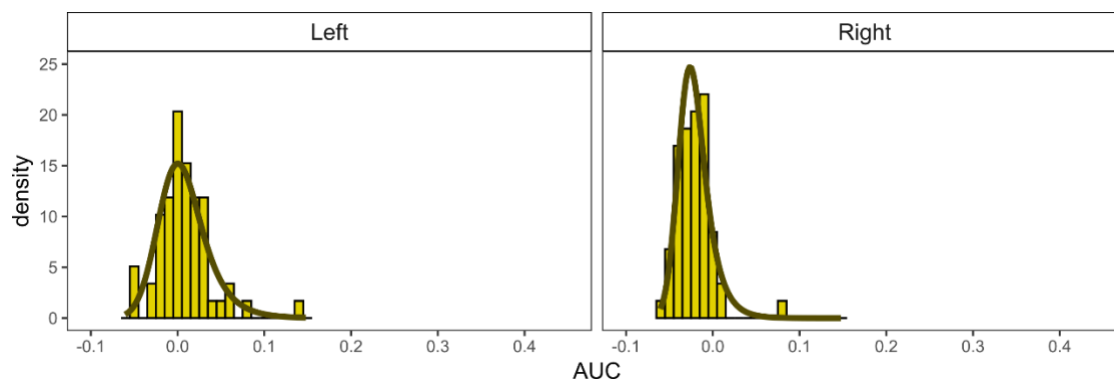
Figure 3-7 shows the distribution of AUC values generated in the baseline, no-choice condition, separately for left and right reaches. The smooth, solid line shows the fit of an ex-Gaussian probability density. The ex-Gaussian form was chosen because the distributions of curvature across choice conditions typically showed right-hand skew and this functional form seems to capture the shape of these distributions quite well. The question is now how well these baseline curves capture the observed distributions of curvature in the choice conditions. If adding a choice component had no effect, the baseline fits (i.e. without any change in the parameters) should be quite good. If the fit is not so good, the question is what aspects of the baseline distribution need to change in order to accommodate the choice effects on reach curvature. In this section, I will test systematically a number of possible modifications of the baseline distribution and assess what modification best accounts for the distributions seen in the choice conditions.

#### *3.3.4.1 Distribution fitting to baseline data*

An ex-Gaussian probability distribution results from the convolution of a normal and an exponential distribution, and can be described with three parameters:  $\mu$ ,  $\sigma$ , and  $\tau$ . The parameters  $\mu$  and  $\sigma$  are the mean and standard deviation of the normal curve, with the parameter  $\tau$  as the decay rate of the exponential curve. To find the best fitting parameters, the likelihood of an ex-Gaussian curve was calculated using the R packages *gamlss* (Stasinopoulos et al., 2021) and *optimx* (Nash et al., 2021) to minimise the negative log-likelihood (using the L-

BFGS algorithm). Three separate starting values for the location,  $\mu$  (-0.1, 0 and 0.1), four separate starting values for the standard deviation,  $\sigma$  (0.02, 0.025, 0.05, and 0.1) and three separate starting values for the exponential parameter,  $\tau$  (0.01, 0.025, and 0.05), were used in all possible combinations, resulting in 36 sets of starting parameters. This wide variation in starting points acts to safeguard against reporting a best-fit where the optimisation routine got “stuck” in a local minimum on the negative log-likelihood surface. The optimised parameters with the lowest deviance ( $-2$  times the log-likelihood) across all 36 runs was chosen as the best fit. The best fitting parameter values for participant four’s baseline distributions are  $\mu = -0.0145$ ,  $\sigma = 0.0198$ , and  $\tau = 0.0222$  for left reaches, and  $\mu = -0.0355$ ,  $\sigma = 0.0118$  and  $\tau = 0.0145$  for rightwards reaches, and describe the curves seen in Figure 3-7.

Figure 3-7 Baseline AUC distributions, with fitted ex-Gaussian curves



Note. Left panel shows the recorded AUCs for baseline reaches to left targets, and the right panel shows the recorded reaches to right targets and the ex-Gaussian curves which was fit to these data.

Clearly there is already considerable variability in the curvature of the reaches which can be attributed to non-decisional influences. Although we know (Figure 3-2d) that the mean AUC measure shifts in the hard choice conditions, it is not clear a) how this shift comes about, and b) how much of the variability in trajectories is already accounted for by these non-decisional influences. Therefore, the question is now what needs to happen with these baseline AUC distributions to turn them into distributions that accommodate the reach curvatures observed in the choice conditions. This question will be assessed by comparing the likelihood of the hard choice curvature distribution under the baseline parameters, with the likelihood of the hard

choice curvature distribution when either individual parameters are allowed to change or all parameters are allowed to change.

Using the parameters from the baseline fit, I can assess the likelihood of the same distribution generating the curvatures seen in the choice conditions. Of course, it is already obvious that there are some differences between the baseline and choice conditions (Figure 3-2). Therefore, an entirely separate distribution may be fit directly to the choice condition data. Freely fitting parameters will naturally fit the choice data better than the baseline fit, but at the expense of a complete, extra set of parameters. It may be possible to obtain a more parsimonious model for the choice data that “inherits” some of the parameters from the baseline model, given that some aspects of the variability in the choice condition will be common to the baseline and choice conditions (i.e. reflecting non-decision influences). By allowing only one parameter for each side to depart from its baseline value, we can ask which modification of the baseline distribution represents the best trade-off between explanatory power (likelihood of the choice data) and parsimony (introduction of additional free parameters).

Figure 3-8 shows the distribution of AUCs for participant 4 in the hard choice condition, separated into left and right reaches. There are five models, each of which vary selected parameters. Each of these can be compared using AIC to assess how the baseline curvature distributions can be modified to account for the choice condition curvature distributions. These models are listed in Table 3-7.

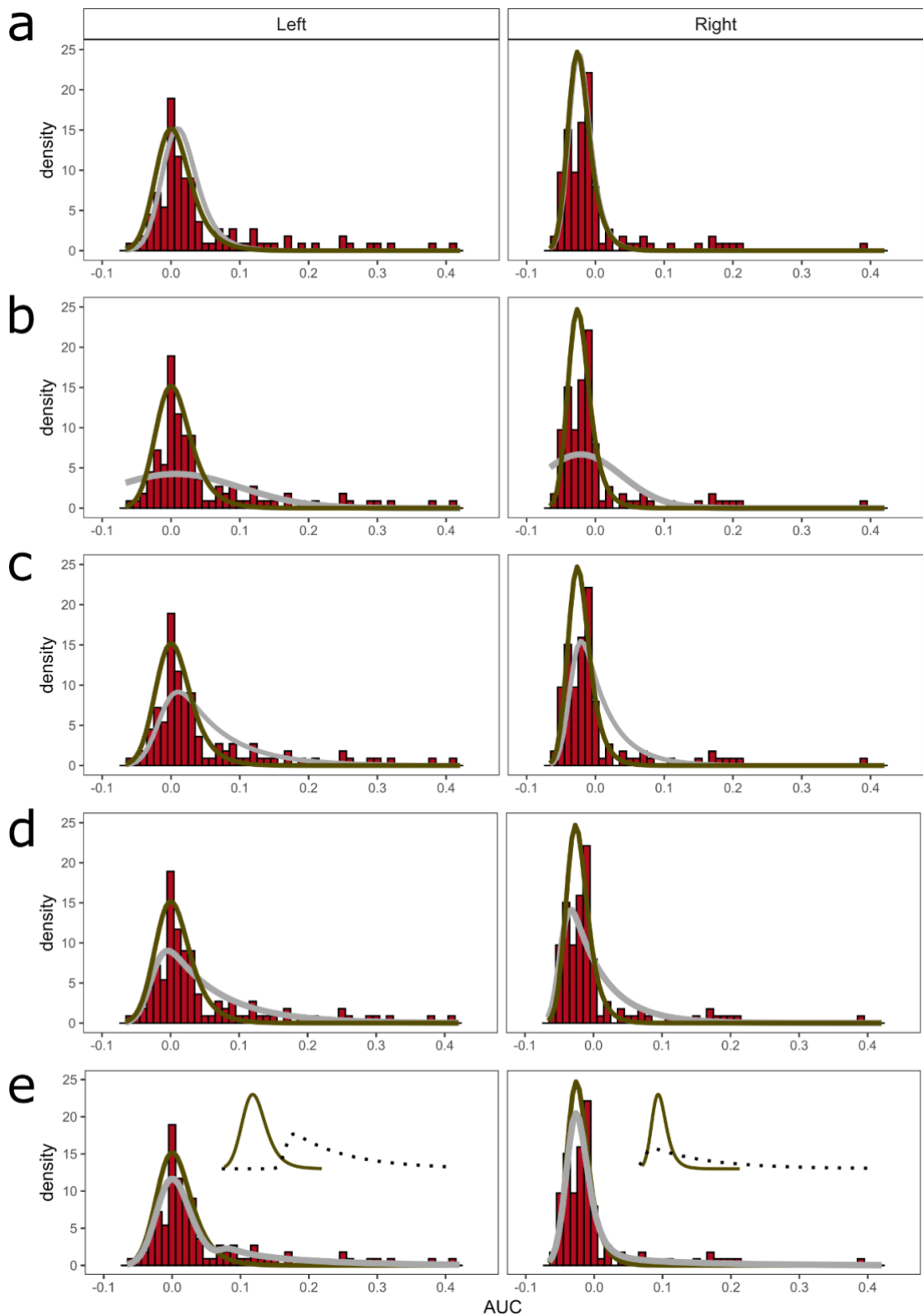


Table 3-7 Descriptions of each model and the free parameters for each distribution model

Model	Description	Free parameters
0	<b>Null model:</b> the baseline distribution parameter fits are assumed to be adequate for the distributions from the choice conditions without modification	0
1	<b>Location shift model:</b> the widths and decay rates of the baseline distributions are inherited, but locations are free to vary	2
2	<b>Scale shift model:</b> the locations and decay rates of the baseline distributions are inherited, but the widths are free to vary	2
3	<b>Decay rate shift model:</b> the locations and widths of the baseline distributions are inherited, but the decay rates are free to vary	2
4	<b>All parameters free model:</b> the location, width and decay rates are all free to vary	6
5	<b>Mixture model:</b> a weighted mixture of the baseline distributions and an additional distribution for each side is fit to the data.	7

Figure 3-8 demonstrates these alternative models for the data from participant 4. Panel a shows the baseline curve described by the Null model, as per Table 3-7 in dark grey and the curve fit when only the location parameter,  $\mu$ , is allowed to change in light grey. Three potential starting values were used, while the scale and tail parameters,  $\sigma$  and  $\tau$ , were kept constant at their baseline values. As can be seen in Figure 3-8a, there is a modest positive change in the  $\mu$  parameter for left reaches, while for rightwards reaches there is little obvious change. The improvement in model fit can be quantified by a reduction in AIC between the null model (0) and the location shift model (1), shown in Table 3-8. Visually, the difference between the baseline distribution and the location-shifted distribution is fairly minor. The correspondence between the hard choice condition and the baseline suggests that a lot of the variability in the choice condition is already captured by a probability distribution with the baseline parameter fit.

Figure 3-8 Best fit probability functions for the hard choice condition curvatures for participant four.



Note. Row a, model 1; row b, model 2; row c, model 3; row d, model 4; row e, model 5. The histogram bars represent the recorded curvature values for participant 4 in the hard choice condition. Overlaid in dark grey is the ex-gaussian curve fit to the baseline reach AUCs, and light grey is the curve generated after the model re-fitting procedure.

This procedure is repeated for the scale parameters, shown in panel b, and the tail parameters, shown in panel c. When the scale parameter is allowed to change, the width of the curve for both reaches is expanded to account for the high curvature reaches in the positive tail of the distribution, as can be seen in Figure 3-8b. When the decay parameter is allowed to change, but the location and scale parameters are not, the tails of both distributions stretch to accommodate the high curvature measurements, as can be seen in Figure 3-8c.

As detailed in Table 3-8, each of these modifications to the probability distribution progressively improves model fit, relative to the null model, as measured by AIC. By allowing all of the parameters to be different to the baseline probability distribution, model fit is substantially improved from the baseline model, and can be seen in Panel d. However, by accommodating the extended right-hand tail of the distributions, the fit misses some of the earlier peak in the distribution. Panel e addresses this short-coming by allowing for these observations in the tails to be accounted for by a separate population altogether. In this case, rather than a single curve, a weighted mixture between the baseline fit and an additional distribution was fit to the data, under the assumption that there are two sub-populations of trajectories mixed into the hard-choice curvature distribution. The starting values for the additional distribution parameter search were the same as those used to seek for the baseline fit, and the starting values for the weight between them was 0, 0.5 and 1.

In Figure 3-8e the dark grey curve shows the original baseline distribution, and the light grey line the mixture distribution. The insets into 3-8e show the two components that go into the mixture (unweighted for the sake of illustration): the baseline distribution and the distribution used to account for the subpopulation of reaches that were affected by the choice requirement. Table 3-8 shows the parameter values for each model, along with the number of free parameters and AIC for each model. For participant four the mixture model provided the best fit, with the baseline distribution contributing 76.5% and the additional distribution 23.5%. It is tempting to

suggest that that 23.5% of the reaches in the hard condition are generated by a different process than that of the baseline reaches, especially given that a similar proportion of reaches by participant four in the hard choice condition (i.e., 22.9%) were identified as “changes of mind”. However, as will be discussed below, the interpretation is not as straightforward as that.

Table 3-8 Parameter fits and AICs for each model variation fit to data from participant four

	Model	Parameter	Left Reaches	Right Reaches	Free parameters	AIC
0	Null model, no change	$\mu$	-0.0145479	-0.0354808	0	-413.22
		$\sigma$	0.0198358	0.0118187		
		$\tau$	0.0221915	0.0145438		
1	Location change only	$\mu$	-0.0050897	-0.0339968	2	-422.05
		$\sigma$	0.0198358	0.0118187		
		$\tau$	0.0221915	0.0145438		
2	Scale change only	$\mu$	-0.0145479	-0.0354808	2	-483.73
		$\sigma$	0.0914646	0.0580999		
		$\tau$	0.0221915	0.0145438		
3	Tail change only	$\mu$	-0.0145479	-0.0354808	2	-700.11
		$\sigma$	0.0198358	0.0118187		
		$\tau$	0.0643535	0.0379461		
4	All allowed to vary	$\mu$	-0.0270702	-0.0502299	6	-729.22
		$\sigma$	0.015884	0.0062873		
		$\tau$	0.0741618	0.0498501		
5	Baseline fit mixed with separate sub-population	$\mu$	0.0686336	-0.0576944	7	-772.62
		$\sigma$	0.005	0.005		
		$\tau$	0.1151258	0.1199044		
		weight	0.2394878			

Note. Table shows which modification model was the best fit for each participant’s baseline curvature distribution to the AUC distribution in the “easy choice” condition. The best fitting model for all participants, except or participant 3, was the mixture model. Note. Table shows which modification model was the best fit for each participant’s baseline curvature distribution to the AUC distribution in the “easy choice” condition. The best fitting model for all participants, except or participant 3, was the mixture model.

Table 3-10 This same procedure was repeated for the easy and hard choice curvature distributions for each of the participants (see Table 3-9 and Table 3-10). The same pattern was found in all cases apart from participant three in the easy choice condition. In this case the best fitting model was the “all parameters free to vary model”.

Table 3-9 Easy choice condition best fitting models

Participant	Best model	Model AIC	AIC weight	Mixture weight	“Change of Mind” percentage
P1	5 (Mix)	-806.64	>0.999	0.161	29.2%
P2	5 (Mix)	-1085.71	>0.999	0.199	14.6%
P3	4 (All fit)	-1089.27	0.982	NA	9.59%
P4	5 (Mix)	-1045.04	>0.999	0.070	12.5%
P5	5 (Mix)	-1088.80	>0.999	0.021	2.92%

Note. Table shows which modification model was the best fit for each participant’s baseline curvature distribution to the AUC distribution in the “easy choice” condition. The best fitting model for all participants, except or participant 3, was the mixture model.

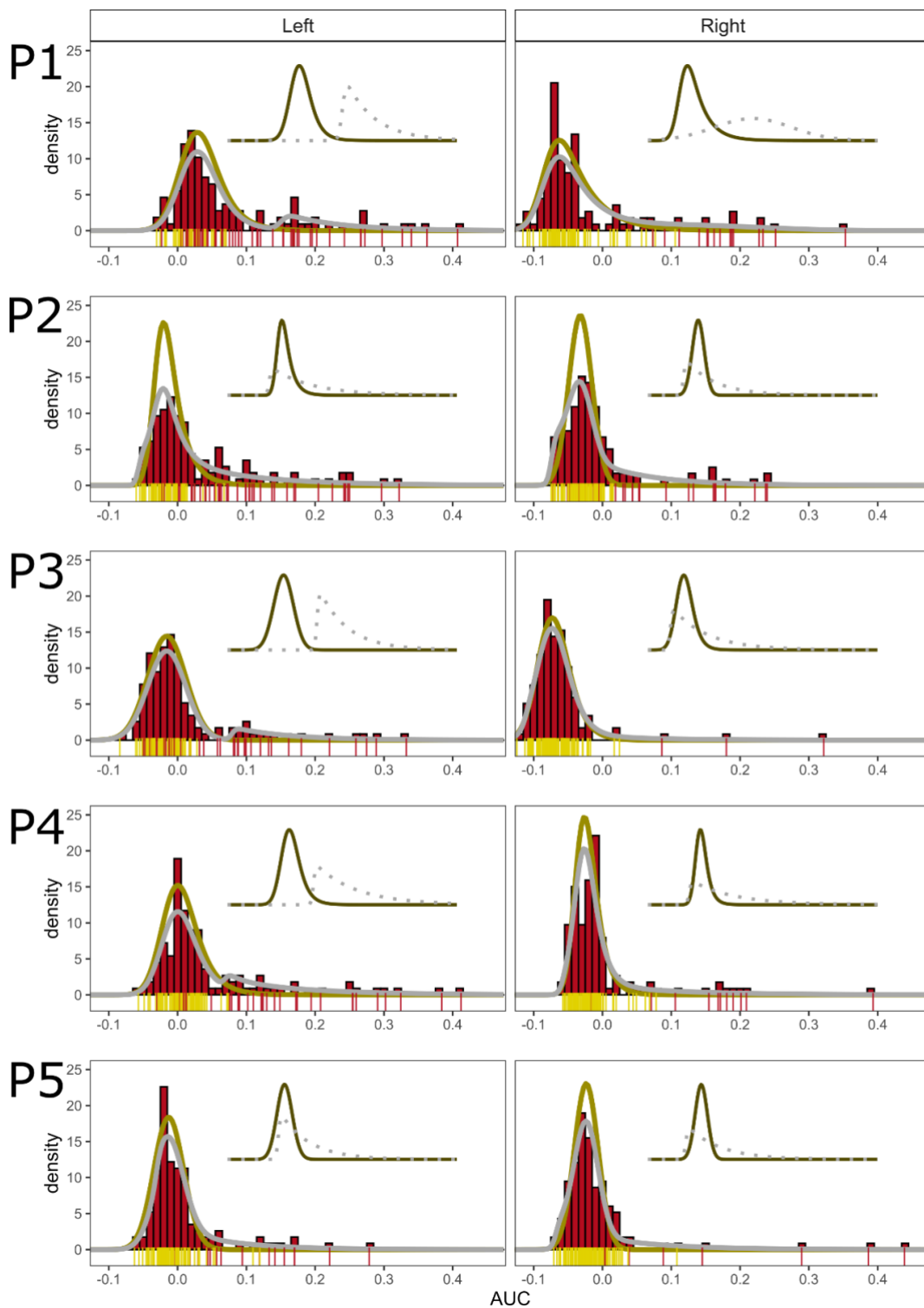
Table 3-10 Hard choice condition best fitting models

Participant	Best model	AIC	AIC weight	Mixture weight	“Change of Mind” percentage
P1	5 (Mix)	-608.73	>0.999	0.196	34.2%
P2	5 (Mix)	-757.98	>0.999	0.567	32.1%
P3	5 (Mix)	-889.67	>0.999	0.143	19.6%
P4	5 (Mix)	-772.62	>0.999	0.239	22.9%
P5	5 (Mix)	-899.39	>0.999	0.319	10.4%

Note. Table shows which modification model was the best fit for each participant’s baseline curvature distribution to the AUC distribution in the “hard choice” condition. The best fitting model for all participants was the mixture model. AIC weight indicates which model, out of those tested, is most likely to be close to the true model on a scale of 0-1 (Wagenmakers & Farrell, 2004).

For all participants the model with the lowest AIC value when modelling hard choice curvatures was the mixture model. As can be seen in Table 3-10, the weighting between the baseline and the additional distributions ranges from 0.14 to 0.57. This means that while the baseline distributions may constitute the major part of the distribution seen for the hard choice condition, there is always a substantial contribution by the additional distribution. Unlike the case of participant four described in detail above, note that the mixture weight does not necessarily match the incidence of “change of mind” trials.

Figure 3-9 Hard choice curvature distributions for each participant, baseline and mixed model fits.



Note: AUC distributions for left and right reaches. Inset plots show each component of the mixed model – solid is the unweighted baseline fit, dotted is the unweighted additional component. Vertical lines beneath histogram show individual trial AUCs, with yellow as the “direct” reaches, and the red the “change of mind” reaches.

Figure 3-7 shows the fits of the mixture model for all participants in the hard-choice condition. The insets again show the (unweighted) components that go into the mixture, with the solid line corresponding to the unmodified baseline component.

As can be seen in the insets of Figure 3-7, in many cases the parameters for the additional component in the mixture models implements a primarily heavy tailed distribution which overlaps with the baseline. However, in other instances (e.g. leftwards reaches for participants one, three and four; rightward reaches for participant one) the additional distribution is distinct. This indicates two processes for reach path generation in choice conditions, one that follows the same pattern as the baseline trials, and a different process for a sub-population of trials. However, this additional process is not *just* capturing the changes of mind, given that the weight of this additional component in the mixture does not match the proportion of change of mind trials (at least, as classified using the criteria adopted here).

### 3.4 Discussion

The primary purpose of this chapter was to replicate results from Chapter 2 and, specifically, to conduct a distributional analysis of reach curvatures, so that the influence of choice processes on reach-to-grasp actions can be estimated separately from the non-decision influences of workspace effects, biomechanical constraints and motor noise.

Linear mixed-effects model analysis results from chapter 2, experiment 2, were broadly replicated, demonstrating that increased difficulty impacted reach duration and curvature. A preference for rightwards targets with the right hand (in right-handed participants) may be expected given findings related to stimulus response compatibility (Lu & Proctor, 1995; Simon, 1990), where targets on the same side as a responding hand are responded to faster than targets contralateral to the responding hand. Additionally, removing change of mind trials from the analysis reduced the main effect of choice difficulty on curvature, though there were still effects of choice difficulty on curvature for some combinations of target location and

orientation. An analysis of initial reach heading revealed a strong preference for reaching to the right hand target, particularly at faster initiation times. Given that the participants in this experiment were right-handed, a right target bias makes sense if they are guessing which is the likely target (and need to start their reach before the 400ms time limit), as this reach direction takes less effort, and whatever action takes less work is typically preferred in free choice reaching studies (Cos, Belanger & Cisek, 2010).

Given the preliminary conclusions available from chapter 2, there were several hypotheses about how baseline distributions would have to be modified to account for changes in curvature distribution induced by the choice requirement. If a smooth modification of the entire distribution of baseline curvatures was adequate to describe the curvature distributions under choice, then we could have concluded that the addition of a perceptual choice process affected all reaches to some extent. On the other hand, if some trials were generated by a different process, such as a change of mind, then there would be two populations of trial curvatures. Overall, across all conditions and participants (bar one), a combination of the baseline reach distribution and an additional distribution provided the best explanation for the reach curvature distributions recorded under choice conditions.

The distributional analyses provided further insights into how responses in choice trials differed to those in the baseline, no choice, trials. The width of the baseline distributions themselves demonstrate the large variability of curvature in trials where there should be no additional curvature related to perceptual decision processes. Therefore, biomechanical and workspace effects on trajectory curvature need to be considered before explaining the effects of perceptual decision-making on reach path curvature. Rather than shifting or stretching the entire distribution of reaches, as may be expected if the presence of an extra target consistently affected reaches on all trials, a combination of the baseline parameters and an additional distribution is required to fit the more complex shape of choice-trial curvature distributions. In



some cases (participants 1, 3-left, 4-left) the additional component did not overlap with the baseline distribution. For all other participants and distributions, the additional component served to add a heavy tail to the baseline distribution.

A natural interpretation of the additional component might be that they capture change of mind trials. Change of mind trials naturally have greater positive curvature and thus dominate the tails of the distribution (and, in some instances, introduce a second mode in the distribution).

Therefore, it is tempting to conclude that the second component in the mixture represents the change of mind trials. However, there are two caveats to this interpretation: 1) the mixture weights do not map onto the proportion of trials classed as changes of mind; 2) the additional distributions span across trials that are not classified as changes of mind. Nevertheless, we may conclude that the majority of trials have trajectories that do not seem to be influenced by the decision process at all – mixture weights range from 0.143 to 0.567 (see Table 3-10). The question is then: which and for what reason are some trials affected by the choice component and others not?

The trials that are not affected by choice will be those where the decision process has either resolved, or the residual influence of choice has become negligible compared to the variability introduced by non-decision influences. In these circumstances the participant may initiate a reach *as if* they are certain about which object is the correct target. No “perceptual decision uncertainty” will be detectable in these reach paths. Three alternative possibilities can explain these curvatures. First, the participant has fully and rapidly resolved the decision process and come to a correct decision using all the evidence available to them. Secondly, the participant is using partial evidence to make a guess about the which target is correct, and that guess is correct. And thirdly, the participant is making a guess based on no information, and that guess is correct. Whatever the case, the second and third of these possibilities will be indistinguishable from the first, at least on the information contained in their overall curvature.

The remainder will therefore be trials where the decision is either mistaken or incomplete when the reach is launched, and there are a range of possibilities that can explain those reach curvatures. First, the participant may have come to a mistaken conclusion about the correct target but corrected that mistake within the reach time. Secondly, the participant used partial evidence to make an incorrect guess about the target but corrected that mistake within the reach time. Thirdly, the participant made a guess *not* based on accumulated information but within the reach time corrected that mistake. Fourth, the participant made an initial reach to an intermediate location based on partial evidence, intending to correct their reach mid-flight. Fifth, and finally, the participant made an initial reach to an intermediate location based on no information from the current trial, intending to correct their reach once sufficient information had been processed. The first three of these possibilities will result in a “pure change of mind” trajectory, while the fourth and fifth represent the conceptions of Friedman and colleagues (2013) and Wong and Haith (2017), respectively.

Given that we have only some trials in which the choice process influences reach trajectories, how does this influence come about? As mentioned in Chapter 1, Friedman and colleagues (2013) suggested a model where partially resolved decisions can influence the first “submovement” of a reach action. If a reach is launched before the decision variable in an evidence accumulator has reached a response boundary, the initial launch is one which averages the motor plans for each target. The weighting between these plans is based on the current state of the evidence accumulator, and the amplitude of this reach is also reduced so that another submovement can be programmed to complete the trial successfully. This model may be able to explain these data. The choice-trial curvatures which resemble those from the baseline cluster are those where evidence accumulation finished before reach initiation. In contrast the additional population of reaches are those where it either has not, or an incorrect boundary was crossed. Visual inspection of the choice trial paths in Figure 3-1 does show some variability in the launch direction, which may be attributable to partial information effects at

reach initiation. The best fitting models for choice curvature distributions were usually those where the additional distribution overlapped with the baseline distribution and with an extended tail. If the decision variable at launch is close to the decision boundary, the correct target will have a strong weighting (in the blend of action plans), but if the decision variable is far from the decision boundary the incorrect target will have a stronger weighting. Since there will always have been time for *some* evidence accumulation before launch, the majority of launches with partial information will be similar to full-information reaches (explaining the overlap), fewer reaches will be launched with equally weighted action plans and only rarely will reaches be launched with the incorrect target dominating the action.

The other potential model to explain how decision-making processes may influence reach paths was that proposed by Lepora and Pezzulo (2015). In this model, decision systems and movement preparation systems are essentially the same, as evidence is accumulated in the activity of competing motor plans themselves. To account for the noisiness of perceptual evidence, an extra mechanism they called a “commitment effect” is implemented which feeds back implicit costs for decision reversals. The combined target for reach actions is the result dynamic interplay between the evidence and the motor execution. This model will be extensively covered in the next chapter, but there are aspects of the data that could be explained by this model. Visual inspection of the reach paths shows that there are occasional trials which “waver” between response options, and paths which are launched with very little information, i.e. straight between the response options.

### 3.5 Conclusion

In conclusion, the experiment and analyses in this chapter further demonstrated that the difficulty of a perceptual choice increases reach curvature. As an extension of the conclusions of chapter two, we have been able to identify that the biomechanical constraints on reach paths, as well as the variability in the motor response, are major sources of variation in reach paths. Any

model which may be able to link reach paths to perceptual decision-making must also at least account for this variability. Of the taxonomy of models presented in the last chapter (Figure 2-1), those which suggest a blending or averaging of motor plans should be considered when linking movement to decision-making, as this can allow for decision-effects on reach trajectories even if there is no change of mind. The next chapter will develop the “embodied” computational model suggested by Lepora and Pezzulo (2015) to link an evidence accumulation mechanism, modelled as a random walk, to a trajectory generation mechanism. Incorporating the variability of baseline trials collected in this experiment will be used to add further realism to the model.

## Chapter 4 Simulating the link between evidence accumulation and reach paths

### 4.1 *Overview*

The earlier chapters in the thesis detail several experiments which aimed to characterise how reach and grasp actions change under increased perceptual uncertainty. From the start the experiments were designed to use a fairly simple perceptual decision for which the computational mechanisms can be approximated using sequential sampling or evidence accumulation models. The experiments are instances of a two-alternative forced choice (2AFC) task, which have classically been used to develop models of speeded decision-making (Ratcliff et al., 2016). However, rather than having the response be the push of a button, which is typical, the response is the temporally extended reaching and grasping movement from a neutral starting point to one of the two targets. Experiments 1 and 2 showed that as decision uncertainty increased, so did the mean curvature of reaches on their way to grasp and retrieve a stimulus object. Experiment 3 demonstrated that while a large amount of variability in choice trials can be attributed to biomechanical and workspace effects, increased choice difficulty remained influential on reach curvature, an influence which could not always be attributed to changes of mind during the reach action. Changes of mind, however, are a strong driver of increased curvature. So far, I have shown that changes of mind are more likely in the hard choice condition in comparison to an easy-choice condition or a no-choice condition. Additionally, the analysis of initial reach direction in chapter 3 showed that the right-handed participants were likely to pick a rightwards reach as a default option. As a result, trials which initially went left but were then corrected to the right target were much rarer than trials which were (incorrectly) initiated to right-targets. This distributional analysis in chapter 3 reinforced this finding – for my participants, in the hard-choice condition, there was a population of reaches whose curvature

distributions resembled those of the baseline trials, and an additional population for which the decision-making process must have had an impact.

This chapter further investigates how target uncertainty, via perceptual uncertainty, may influence reach-to-grasp action should there be as strong a coupling between an accumulating decision process and reach paths as suggested by Lepora and Pezzulo (2015). To that aim a drift-diffusion model of decision-making, for which a random walk is a discrete time approximation, is described and a way to link the trajectory of the hand with properties of the decision process is developed. The output of the computational model is simulated by varying the parameters singly and in combination, and the biomechanical and motor noise variability is incorporated using empirical data collected in experiment 3. An alternative to the model is also presented which could, in principle, account for curved trajectories which are generated by modifying the starting point for evidence accumulation or changes of mind.

## 4.2 *Introduction*

The classic “serial” approaches to decision modelling assume that all relevant decision processes will be finished before any response is executed (Hurley, 2001) appears inadequate as a process that could generate the kinds of results seen so far; particularly in contrast with embodied cognition approaches suggest that the decision and the action are intertwined (Gordon et al., 2021). This classic assumption is understandable when the decision is categorical, and the action required irreversible and unmodifiable. However, as outlined earlier in this thesis the assumption may not apply when the decision process is reliably dynamic and the action is a large reach-to-grasp movement. A straightforward model of decision and action in a two-response task, which needs only to link the results of a decision process to the specification of a motor plan, will therefore only generate trajectories which go directly to either one or the other target. Though noise in the process of movement planning and execution will lead to variability between repeated actions (Shi & Buneo, 2012), systematic curvature due to motor interference

from a competing alternative (i.e. a non-target in the preceding experiments) will not occur in such a system, or under relaxed timing conditions (Welsh et al., 1999).

The simplest way to implement a model which can use the output of static (or at least closed-off) decision processes to generate deviating trajectories would be a change of mind model (*Figure 1-7*; *Figure 2-1*; also see also Lepora & Pezzulo, 2015; Resulaj et al., 2009). To do this, the trajectory formation algorithm could be much like that suggested by Flash and Henis (1991). A motor plan, optimised to minimise jerk, would be specified to move the hand from the start location to one target and moments later a second motor plan to move the hand from the original target to the new target would be superimposed on top of that. The mechanism of the decision process for this kind of linkage would not particularly matter – static decisions are passed forward from the decision system to activate a sequence of single motor plans. Perhaps the first decision was a fast but incorrect guess (Ollman, 1966), or a short run of VTEs (Audley, 1960), or the threshold signals from a continuing accumulator process (Resulaj et al., 2009). However, the reader may recall from Chapter 1 that average intermediate trajectories could be generated with the later superposition scheme which biased the original reach heading when the target switch happened in a critical window before movement preparation (Henis & Flash, 1995). However, recall too that accumulator models include a period of non-decision time after a boundary crossing assigned, in part, to separate the movement preparation process and the action execution process (Ratcliff et al., 2016); if early incorrect boundary crossings still influence movement preparation, then so might the far more frequent correct boundary crossings. With just direct and revised trajectories produced in this way an averaged trajectory would be a mixture of such direct and corrected trajectories, with only the more complex version able to generate the kind of smoothly curving intermediate trajectories from mouse tracking. Static decision processes and serial motor preparation processes are sufficient to support the implementation of this model.

A slightly more complex version is the intermittent submovement control model of Friedman and colleagues (2013). The perceptual decision mechanism in this case is a two-choice accumulation to bound model augmented with a separate one-sided timing accumulator. A motor plan for each potential response action is prepared in parallel, and if the choice diffusion process finishes first a single motor plan is selected and executed. If the timing accumulator finishes first the reach is launched with a blended action plan. The balance between the decisions determining the angle of the first submovement, and the distance remaining between the decision variable and the boundary determining the amplitude of the movement. This model suggests both dynamic decision processes and the maintenance of multiple motor plans, however the flow of information between internal processes and external action is limited by the time delays inherent to innervating the muscles to execute motor actions (Liao & Kirsch, 2014).

A final possibility which also rests upon interacting dynamic processes is the Lepora and Pezzulo (2015) “action preparation with commitment” model. Lepora and Pezzulo (2015) developed the model to simulate 2D mouse movements and explain both average curvatures and the speed-accuracy trade-off observed in data from a lexical decision-making task (Barca & Pezzulo, 2012). The model explicitly formalises some of the core assumptions of embodied decision making; decision processes and movement preparation and execution are not separate, and a decision is now only final when the action itself is complete, rather than the crossing of an unobservable neural Rubicon. Given the neurophysiological and behavioural findings reviewed in Chapter 1 (see also Cisek, 2007), the continuous flow of noisy perceptual information directly into movement systems may be a feasible link. Extending the model using the baseline curvature distributions from Chapter 3 may allow the model to not just simulate mouse movement trajectories, but also real reach-to-grasp trajectories. The remainder of this chapter discusses the model mechanisms, adapts the model and explores how the curvature distributions generated by the model change as the parameter space is explored. Finally, the impact of including



baseline data is assessed. The aim here is to explore whether this model scales up to the more naturalistic reach-to-grasp movements that are the focus of the experimental work in this thesis.

#### *4.3 Linking decision theoretic models and reaching trajectories*

Lepora and Pezzulo (2015) operationalised the link between the noisy perceptual evidence and the trajectory by translating the current state of the decision variable directly into blended reach direction. Weighted according to the value of the decision variable at any one instant, reach movements will be towards a position between the two targets. This simple continuous flow between the random walk and the movement focus (the target blending model) will not on its own always generate realistic trajectories: the “noisy” decision variable can sometimes fluctuate wildly, but these fluctuations are not seen in real reach paths which smoothly “home in” on the target, so an additional mechanism is needed. Drawing on ideas from embodied cognition, in which information about the arm position itself is treated as a source of evidence pointing to one or the other target, Lepora and Pezzulo implemented a mechanism they termed the “commitment effect”, and how this is implemented will be detailed in the next section. This mechanism acts to smooths out the simulated trajectories from the noisy activity of evidence accumulation, and receives theoretical support from the idea that there is a build-up of activity in pre-motor and motor cortices which correlates with the moment that deliberation between ambiguous targets is resolved, but does not correlate with a build-up of evidence (Thura & Cisek, 2014). Cisek and Thura (2014) use neural evidence for a commitment effect to argue against the traditional drift-diffusion decision model, and in favour of an urgency-gating model. This makes sense within the framework of embodied decision-making where the “decision boundary” is no longer a hard cut-off after which the decision is made, but represents instead a decision-makers level of caution. This model implements the continuous flow assumption that is implicit in much of the mouse tracking literature and demonstrates that additional mechanisms are necessary in order to link the decision variable to the movement trajectory.

The output of the simulations are the curvature metrics in the form of the familiar AUC measure. To get to this point it is worthwhile to detail in stages how the model is constructed from random walks, translating those into a target-blending simulated reach, and then incorporating the commitment effect. Once a reach has begun, the commitment effect is implemented as feedback from the motor system which biases the accumulation of evidence toward whichever target is closer at that point in time. This has the effect of penalising late revisions in target selection. Since the brain is simultaneously weighing the need for making the right decision and the need for completing the action in a timely and energy efficient way, late revisions may unnecessarily sacrifice speed for accuracy. Late in any reach a greater directional change is necessary, and the energy and time cost of decision revision may be too high.

#### 4.3.1 Stage 1: Generate random walks

The drift diffusion model is a continuous time extension of the discrete time random walk model, in which evidence for a proposition (classically A or B, or A or A') is sampled sequentially and integrated over time. As such the first stage in modelling the flow of uncertainty from perception to action is generating a random walk for each trial. If uncertainty at this level is translated directly to the reach movement, then the state of the decision variable before a boundary is reached will inform the trajectory of the hand in some way.

Each random walk is generated as a vector  $\mathbf{z}$  with a mean drift rate of  $u$  and a noise level of  $\sigma$  where  $\varepsilon = \mathcal{N}(0, \sigma)$ :

$$z_t = \sum_{t=1}^t (z_{t-1} + u + \varepsilon) \quad \text{Eq. 4.1}$$

In the standard diffusion model, a decision starts at a value close to 0 and is terminated when the decision variable crosses an upper or lower boundary. The upper boundary is typically  $b$ , and the lower boundary is  $-b$ . As we need to have the simulated agent act before a decision is fully

resolved (either correctly or incorrectly), random walks are generated up to  $t=500$ , rather than halting at a threshold. This accounts for the idea that that decision completion is now instead defined as *action* completion while also allowing early crossings of the lower boundary to continue to accumulate if action is ongoing. As a result, the modelling of process termination is moved into the trajectory generation algorithm.

#### 4.3.2 Stage 2: Generate trajectories using an action focus

To generate trajectories using a decision variable that has not yet reached either boundary, the reach must begin before any boundary is crossed with the target of the reach aimed at a position colinear and between the two targets, weighted according to the strength of the evidence at that time. If the decision variable is above the upper boundary (representing target 1), or below the lower boundary (representing target 2), then the action focus is the target.

These assumptions can be formalised as the action focus at time  $t$ :

$$(x(z), y(z))_{focus} = \begin{cases} (x_1, y_1), & z > b \\ \frac{|b-z|}{2b}(x_1, y_1) + \frac{|-b-z|}{2b}(x_2, y_2) & -b < z < b \\ (x_2, y_2) & z < -b \end{cases} \quad \text{Eq. 4.2}$$

Note that the time dependence in this equation is implicit in the decision variable  $z$ . As the decision variable drifts towards  $b$  or  $-b$ , so will the action focus. At each time step the effector moves towards the action focus by a set distance,  $v$ . The reach, and the decision, is terminated only when the effector is sufficiently close to either target position.

#### 4.3.3 Stage 3: Feedback the position of the effector into the decision variable as a commitment effect.

As formalised so far, the model at this stage does not create realistic trajectories. Depending on the noisiness of the random walk relative to the boundary separation, the action focus can fluctuate rapidly between the target locations. Trajectories generated like this will be seen to

wobble near the start of the reach, but nearer the end may spend much time in a state of indecision. The commitment effect overcomes this problem by having the position of the effector itself influence the decision variable. This is achieved by augmenting the value of the decision variable,  $z$ , fed into equation 4.2 with information about the relative distance between the current effector position and the two targets. The influence of this effect is modified by the gain parameter,  $g$ , as formalised in equation 4.3.

$$z_{com}(t) = z(t) + g \frac{d_2 - d_1}{d_2 + d_1} \quad \begin{array}{l} d_1 = |(x, y) - (x_1, y_1)| \\ d_2 = |(x, y) - (x_2, y_2)| \end{array} \quad \text{Eq. 4.3}$$

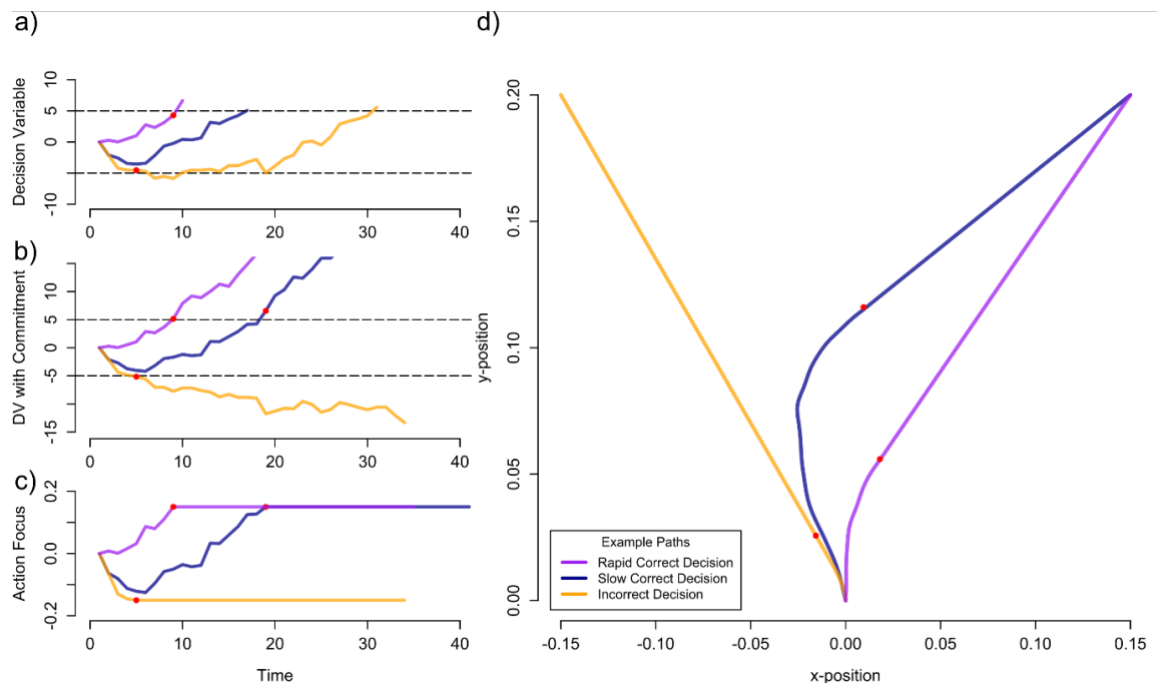
The ratio  $\frac{d_2 - d_1}{d_2 + d_1}$  in the equation above reflects the relative distance of the effector to each of the two targets on a scale from -1 to 1. At the start of the process the effector is equidistant between the targets so there is no commitment to either one, however as the effector moves forwards the decision variable is biased further towards whichever target is closest. One way to think of this is that the commitment effect adds evidence in favour of the target that is currently closer, and this effect strengthens as the reach continues. This mechanism reduces the tendency for trajectory alterations later in the reach process and effectively implements a time limit on the decision; even if the random walk would not have crossed either boundary the reach action will be over with the decision completed.

#### 4.3.4 Stage 4: Calculating the AUC curvature metric for each simulated trajectory

With a trajectory trace deterministically associated with each instantiation of a random walk, AUC values can be calculated in an analogous manner to those in the experimental data. The straight-line path between the origin and the target is scaled to unit distance, and the polygonal area between the trajectory and straight line is the AUC. Figure 4-1 panels a-c shows three examples of how a discrete time random walk is translated into the action focus, with the final trajectories shown in Figure 4-1d. The purple line shows a decision and reach that rapidly found its way to the target. The blue line shows a decision and reach that found its way to the correct

target, but with a large deflection towards the distractor. The orange line shows a reach that rapidly found the incorrect target.

Figure 4-1 Three realisations of the continuous flow with commitment model.



Note. Figure shows three random walks and the process that turns them into trajectories (d) in the model based on Lepora and Pezzulo (2015). Panel (a) shows the unmodified random walks. Panel (b) shows how those walks are modified using the commitment effect gain. Panel (c) demonstrates how that once the action focus is either target, no further target modification takes place. The red dots in panels a-c indicate the time step at which the action focus is reached. Panel (d) translates this into the workspace coordinates for simulated reaching movements.

The model used to generate the random walks in Figure 4-1 had the mean drift set to a value of  $1/3$ , and the diffusion noise set to 1. The upper decision boundary is a correct decision, while crossing the lower boundary would (in classical drift modelling) represent an incorrect decision. With the decision boundary set at  $\pm 5$  the mean walk will cross the upper boundary within 20 time steps (200ms, given a timestep of 10ms in these simulations). Panel (a) plots the random walks used as the input into the trajectory generation process across time. Panel (b) plots the decision variable with the addition of the commitment effect across time.

Once a reach has begun, the commitment effect is feedback from the motor system which penalises late revisions of the decision by introducing bias according to the distance of the

effector to the target. Since the brain is simultaneously weighing the need for making the right decision and the need for completing the action in a timely and energy efficient way, late revisions may unnecessarily sacrifice speed for accuracy. Late in any reach a greater directional change is necessary, and the energy and time cost of decision revision may be too high.

Panel (c) plots the position of the “action focus” for each trajectory across time. The y-axis no longer represents an abstract variable in the perception-action system, but the lateral position on the line between the two targets that the reach is headed towards, and is now measured in metres, rather than arbitrary units. As such a correct decision is a now reach to the right, and the y-position of the action focus is limited to the target location. Each line plateaus when the target of the reach is no longer going to change.

Panel (d) shows the full simulated trajectories for the three example decisions, with the axes of the chart representing the xy coordinates of the simulated effector during each trial (in metres). The red point on each trajectory is the point in time that the action focus is no longer shifting as the decision variable combined with the commitment crosses a boundary in panel (b). Each simulated reach starts at coordinate (0,0) and moves with constant velocity (0.0076 m/timestep; calculated from the overall mean velocity for reaches in the data from experiment 3) towards the action focus. The simulated reach is terminated once the effector is at its closest point to the target. The trajectory is then scaled and rotated to start at precisely 0,0 and end precisely on the target location.

Once a trajectory has been created in this way, we can treat it similarly to the reach data collected in the earlier experiments and calculate its curvature using the same signed AUC procedure. The next section systematically explores the effect of changing these parameters.

## 4.4 *Parameter Exploration*

The data from Experiments 1 – 3, shows a grouping around or close to zero for AUCs with a long tail. The initial aim here was to explore the parameter space of the model to assess qualitatively whether it can produce these kinds of AUC distributions.

Drift (in DDMs) is, as the name suggests, a fundamental feature of the models. The average drift rate,  $\mu$ , is a parameter set by the researcher or fit to a dataset and represents the rate of evidence accumulation uncorrupted by noise. In the DDM, the drift represents the strength of net evidence between the two alternatives. It is typical in this scenario to have a set decision boundary  $b$  at  $+b$  and  $-b$  for the correct and incorrect choices respectively, and to start accumulating evidence from 0. When applied to standard RT and accuracy data, increasing the separation between the boundaries makes participants slower, but more accurate.

In the following section, I will explore the effects of changing these two parameters—drift and boundary separation—on the curvature of the reach trajectory. I will also explore the effect of changing the gain parameter that modifies the strength of the commitment effect. Note that the gain is not a parameter of the standard diffusion model, but the separate feedback mechanism added by Lepora and Pezzulo (2015) to model mouse movement trajectories. Finally, I will look at interactions between pairs of parameters (drift and gain; decision boundary and gain; decision boundary and drift).

### 4.4.1 Single parameter variations

Table 4-1 describes the parameters varied in the following simulations. When one parameter was varied the other two were held at a constant value, also listed in the table. The values within each range were chosen such that a change in the distribution shape was visible in the chart.

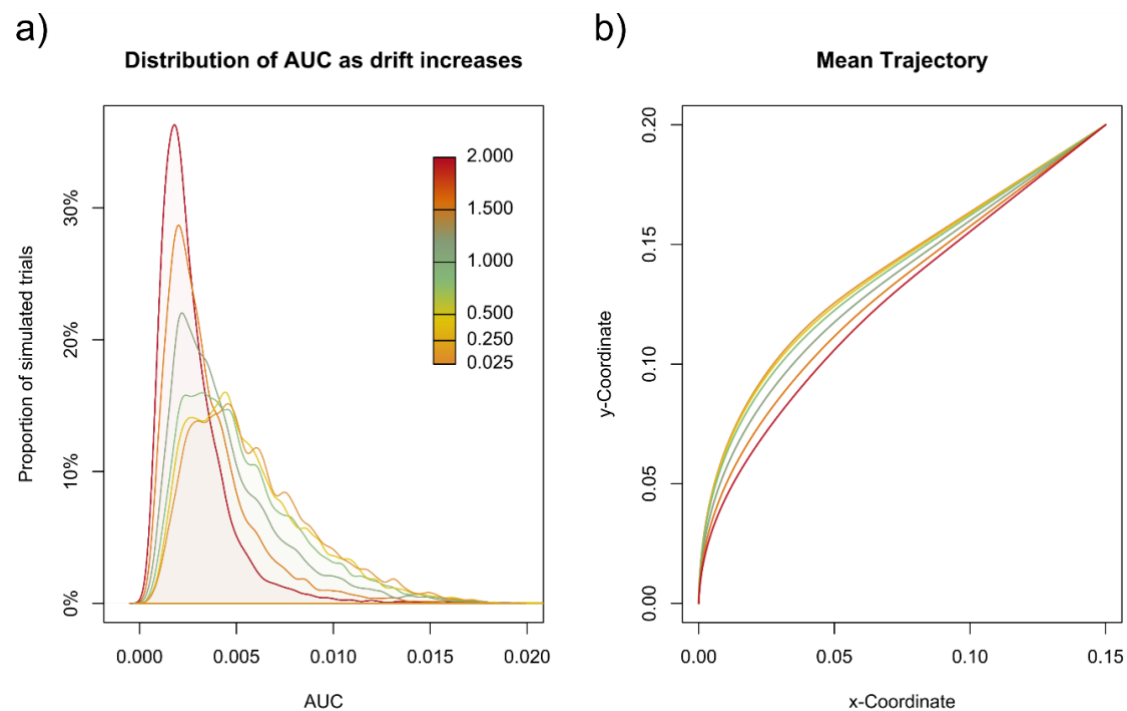
Table 4-1 Single parameter variations in decision model

Parameter	Symbol	Description	Range of Values (Min; Max)	Value when held constant
Drift rate	$\mu$	The average rate of evidence accumulation in arbitrary units.	0.025; 2	1
Boundary	$b$	The height of the decision boundary in arbitrary units	1; 100	7
Gain	$g$	The multiplier applied to the commitment effect, which feeds back into the decision variable as it approaches the decision boundary	0; 10	4

Figure 4-2 shows the results of simulations in which the drift parameter was changed from 0.025 to 2. For each value of the drift parameter, 10000 simulated trials were generated with “unsuccessful” trials (those where the simulated reach terminated on the incorrect target) filtered out. Figure 2a shows how the mass of the distribution of curvatures becomes increasingly squeezed towards zero as the drift rate increases. Figure 2b plots the overall mean trajectories from simulations, and shows that higher drift values lead to more direct paths, while lower values increase average curvature in the middle part of the trajectory. This behaviour is to be expected: a low drift rate represents greater uncertainty about the correct target and the decision variable will hover around the starting point for longer. When translated into the action focus, the effector is at least initially aimed at a point in between the two targets.



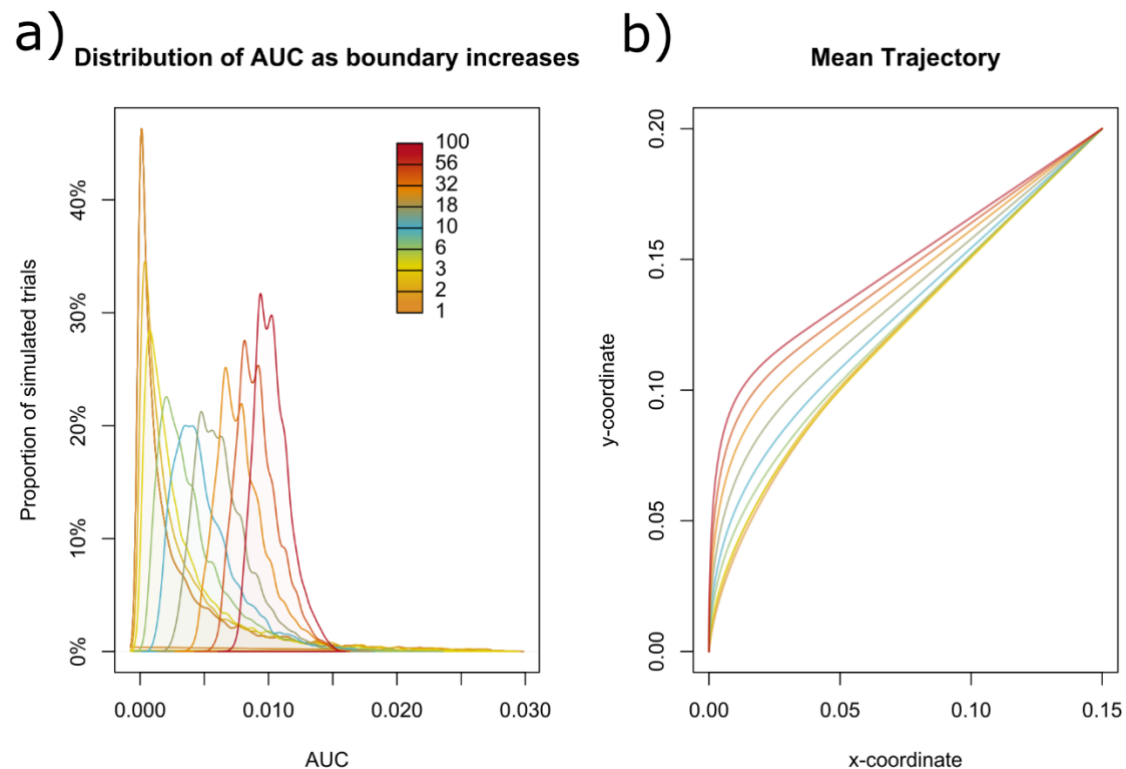
Figure 4-2 Simulated AUCs and mean trajectories contingent on drift rate.



Note. Charts show simulation results when the drift parameter was adjusted – colours represent the drift value used in each simulation. Subplot (a) shows the distribution of curvatures, while subplot (b) shows the average trajectory from each run of simulations. Low drift parameters lead to overall greater curvature.

Figure 4-3 shows the distribution of AUCs and mean trajectories from 10000 simulated random walks with each line representing a different value for the decision boundary in the model. As the boundary increases the action focus remains in between the two targets for longer, translating into more curved trajectories, represented by a rightward shift in the AUC distributions.

Figure 4-3 Simulated AUCs and mean trajectories contingent on boundary separation value.

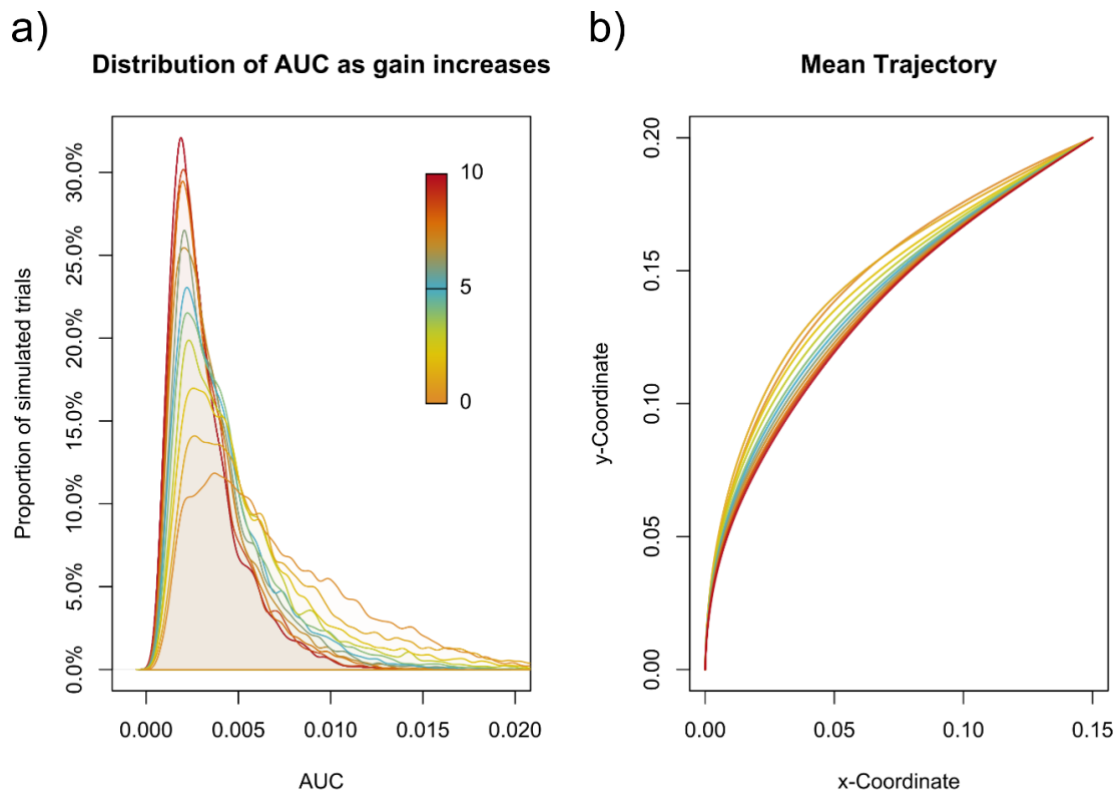


Note. Simulation results when the boundary parameter was adjusted – colours represent the boundary value used in each simulation. Subplot (a) shows the distribution of curvatures, while subplot (b) shows the average trajectory from each run of simulation.

Figure 4-4 shows the distribution of AUCs and mean trajectories from 10000 simulated random walks with each line representing a different value for the gain parameter in the model. A stronger commitment effect reduces the variance of curvatures and pushes the mass of the distribution towards zero. This behaviour is expected because if the gain is large a relatively small bias in the evidence in favour of one option will be amplified and reinforced. As a result, it is more likely that the decision boundary for that option is reached more quickly, after which the reach will go directly to the corresponding target. The effect of the gain does require some

evidence build-up before it really manifests itself in the reach trajectory, which can be seen by the “fanning out” of the mean trajectories in the middle and later parts of the reach.

Figure 4-4 Curvature distribution and mean trajectory as commitment gain varied.



Note. Simulations results when the gain parameter was adjusted – colours represent the gain value used in each simulation. Subplot (a) shows the distribution of curvatures, while subplot (b) shows the average trajectory from each run of simulation.

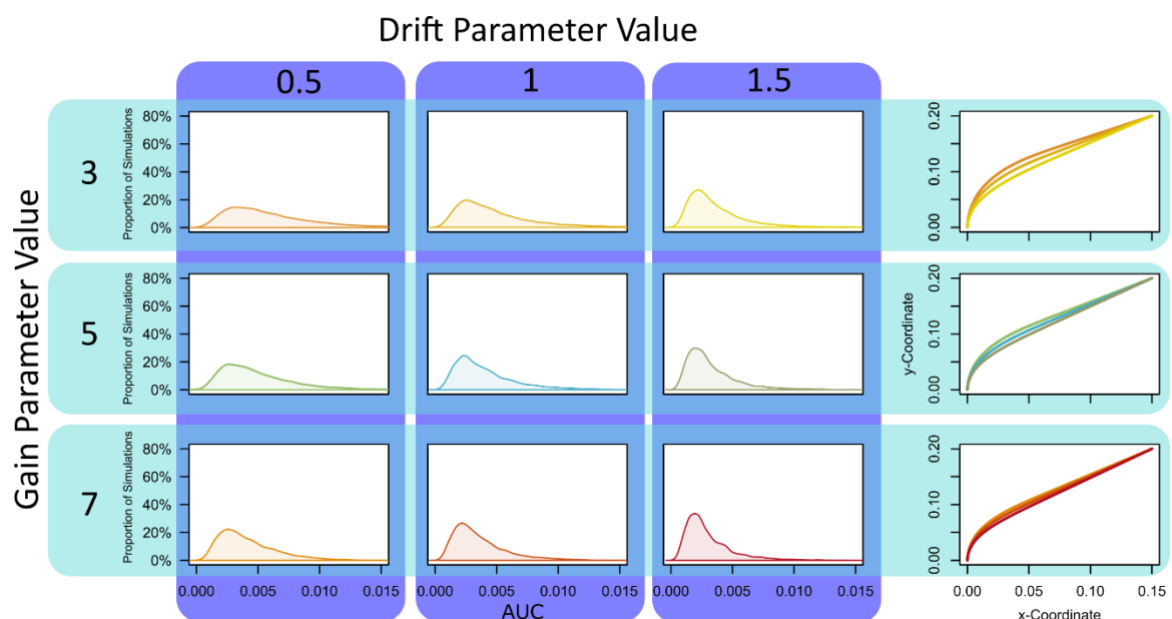
All three parameters change the curvature of the trajectories, and the distributions of those trajectories in slightly different ways. A high drift rate resolves the decision quickly, reducing the variance and flattening the overall curvature, while a low drift rate spreads the distribution out. A similar effect is seen as the gain parameter is increased, though the increase in curvature seems to be more to the middle of the trajectory. Increasing the boundary parameter to extreme values has the effect of shifting the distribution in the positive direction and straightening out the early part of the trajectory.

#### 4.4.2 Parameter interactions

To find parameter values that may lead to reasonable simulations of reaching under perceptual uncertainty, we should consider how the parameters interact. In

Figure 4-5, below, both the drift parameter and the gain parameter are adjusted, with the corresponding AUC distributions and mean trajectories plotted. As can be seen from the distributions, increasing drift reduces the number of larger AUCs, but at higher gain values there is already a tighter cluster of AUCs nearer zero, so changing the drift parameter has less of an influence. The commitment gain effect exerts a stronger influence as the simulated effector moves towards the targets, thus the simulations with a higher gain have less opportunity vary later in the reach.

Figure 4-5 Curvature distributions and mean trajectories as drift rate and gain are varied.

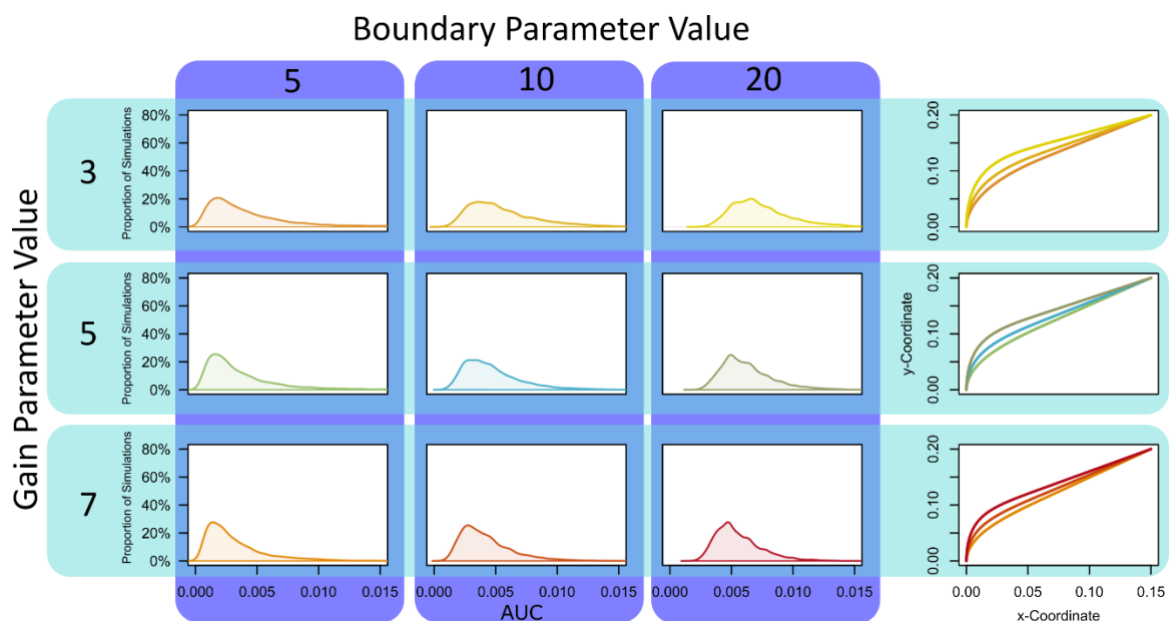


Note. Three gain parameters (3, 5, 7) and three drift parameters (0.5, 1, 1.5) are shown. Decision boundary parameter for these simulations was set to 7.

Figure 4-6 follows a similar format, but in this case the gain and decision boundary parameters were varied. The parameters commitment gain and decision boundary do not seem to interact strongly. As the boundary increases, the central tendency of the distributions moves to the right. With increased gain there is a slight queezing of the distribution to the left. The boundary and

gain have complementary effects on the distribution and mean trajectories. As the gain on the commitment effect is increased simulated trajectories straighten out towards the target, while as the decision boundary increases the trajectories tend to spend more time moving toward the midpoint of the targets.

Figure 4-6 Curvature distributions and mean trajectories as boundary and gain parameters are varied.

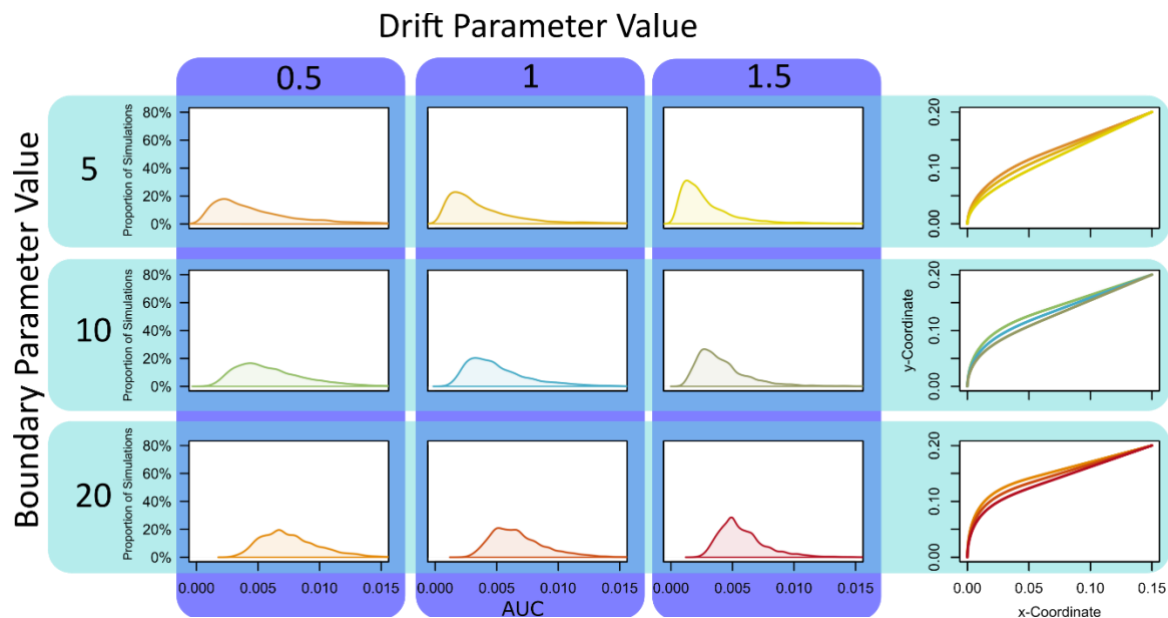


Note. Three gain parameters (3, 5, 7) and three boundary parameters (5, 10, 20) are shown. The drift rate in these simulations is set to 1.

Modifications of the drift rate and the decision boundary are common when fitting standard accuracy and reaction time data with the drift diffusion model. In Figure 4-7 the decision boundary and drift rate are varied systematically. As can be seen, an increase in drift rate implies less competition between the two targets, with stronger evidence in favour of the one target, or movement plan, over the other. A random walk with a greater drift rate will naturally pass the decision boundary faster, and manifests in this model through the simulated trajectories straightening out earlier on in the reach action. As the noise in the accumulator is kept constant, the signal-to-noise ratio is relatively higher for stronger drifts. Conversely, lower drift rates will mean that the diffusion noise has a much greater influence, particularly when boundary

separation is also narrow – this results in a greater proportion of erroneous completed reaches while those that do succeed will have greater variability in curvature.

Figure 4-7 Curvature distributions and mean trajectories as the decision boundary and drift rate were varied



Note. Three decision boundary values (5, 10, and 20) and three drift values (0.5, 1 and 1.5) are shown. The commitment gain value was set to 4 for these simulations.

Taken together, the drift, boundary and commitment gain parameters each modify the mean curvature and the shape of the curvature distribution.

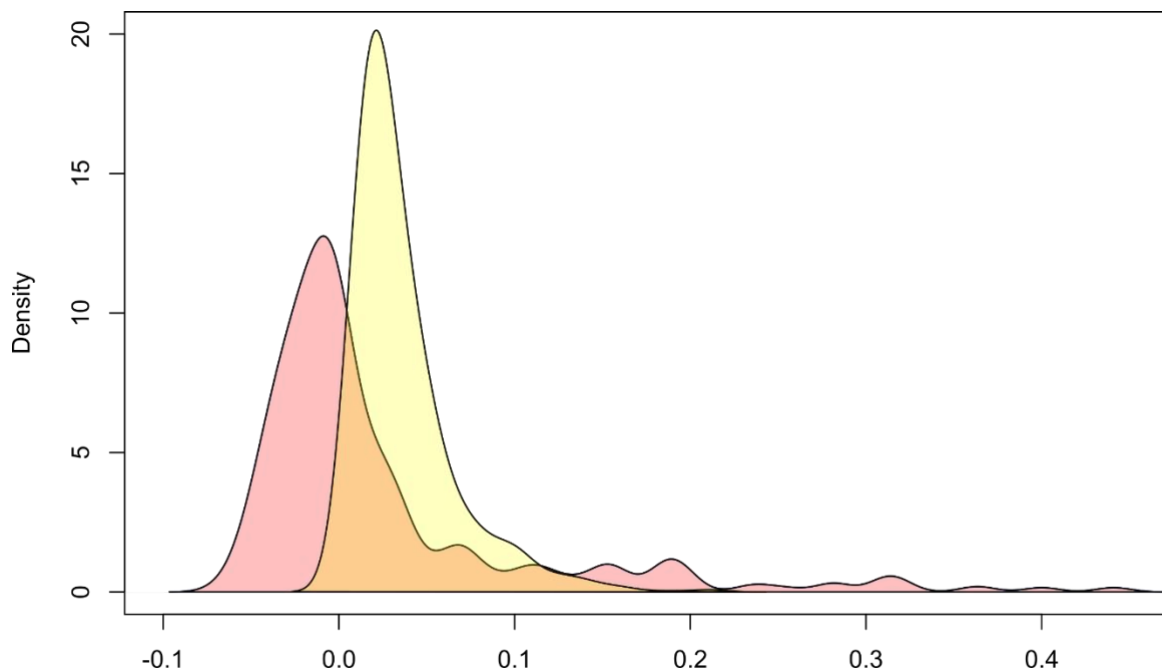
#### 4.5 Adapting the model to accommodate variability from biomechanical constraints and workspace effects.

As demonstrated above the model potentially accounts for reach trajectories that curve towards the distractor while on their way to the correct target. However, the continuous flow model only generates curvature towards the competing target and, depending on the parameters of the model, there may be very few which have little if any curvature, as with the more direct reaches seen in both the baseline and choice conditions. Add to this the negative curvature seen particularly on rightwards reaches in the empirical data, and it is clear that without taking the

biomechanical constraints of the task into account the model, in its current form, will struggle to generate data similar to that recorded from participants.

To illustrate this point, Figure 4-8 shows the distribution of the empirical data, gathered from participant four's hard choice-trials (in red). These observed trajectories contain curvature in both positive and negative directions with a long and shallow tail of movements that curve strongly towards the non-target. In contrast, the yellow distribution shows an example distribution generated by the model explored above, with a large peak slightly above zero, and a tail which is shorter and with a more even drop-off from the mass of the distribution. No exhaustive parameter search was conducted to maximise the goodness-of-fit for this curve. However, the parameter exploration above provides a good clue about what the closest possible approximation might look like in this model. The distribution shown in yellow, while undoubtedly not the "best" fit, is a representative example that meets these criteria.

Figure 4-8 Hard-choice distribution (participant 4) and a simulated curvature distribution using the continuous flow with commitment model



Note. Kernel density plots show the hard-choice trials for participant 4 (blue) and an equal number of simulated trials (yellow). The simulated curvature was generated with a drift rate of 1.5, a decision boundary of 5, and a commitment gain of 5.

Two related problems which stem from the model's assumption that the reach path is entirely governed by the noisy decision process. As a result, the simulated effector only ever moves towards a blend of the target locations, which gradually resolve to one of the target positions. First, target blending is necessary for these simulations to show *any* curvature, but this mechanism necessarily implies that curvature will always be in the direction of the non-selected target. Hence, we need to include in the model a mechanism that allows for simulated reaches with negative curvature, without removing the ability of the model to account for decision uncertainty during the reach movement itself. Second, the model currently attributes all the variability in the reach paths to the ongoing resolution of target uncertainty. The model does not contain any other sources of noise that are known to introduce variability in movement trajectories, such as basic motor noise (van Beers et al., 2004) and the motor system's utilisation of redundant degrees of freedom to maintain performance in the presence of such noise (Krüger et al., 2017).

With regards to the first problem, there are existing models of trajectory curvature in eye movements (Meeter et al., 2010) and reaching movements (Tipper et al., 1994) which suggest that locations are encoded by populations of units on a motor map. When these locations are sufficiently close to each other the location coding units overlap, and since selection of one target involves inhibition of the other, some units for the target location are also inhibited. Initial movement direction may thus be biased away from the non-target. It is possible that this inhibitory mechanism on a motor map representing the two possible targets is responsible for the negative curvature observed in the choice data from the reaching experiments (cf. Figure 4-8). However, note that even in the baseline conditions from every participant there are trials that curve away from the empty non-target location. On these trials there was no decision to be made, as there was only one target to pick up. It may be that participants inhibited an empty location, given that both locations were task-relevant and fixed throughout the experiment. Moreover, reaches on these trials also show considerable variability in curvature, suggesting that



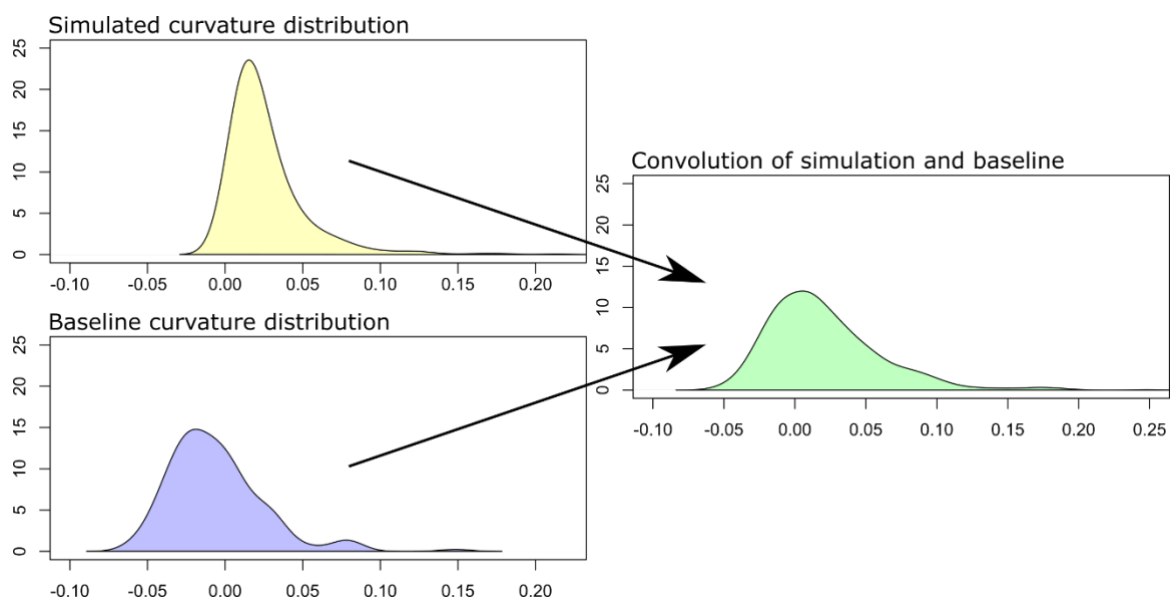
not all variation in the trajectory stems from decision noise. A more likely explanation is that motor noise is a dominant form of noise in this type of task. It introduces initial deviations towards and away from the (empty) non-target location and the correction of these initial deviations produces curved trajectories even without any competition between two potential movement programmes. Moreover, biomechanical constraints may produce systematic curvature in the trajectories simply as a result of the constraints of the workspace and the initial position of the arm. Clearly such biomechanical constraints and motor noise are not represented in the model explored above. Given that the model was developed to account for mouse movement trajectories, it is possible that these constraints do not apply to mouse movements, where the arm remains largely stationary and most of the movement is performed by rotating the wrist in just one plane.

In other words, the model needs to contain both decisional and non-decisional effects on the trajectory. Rather than endowing the model with biomechanics and additional sources of noise, I took the following approach: The baseline condition from experiment three is assumed to represent only the curvature that would be expected in the absence of any decision-related effects on the trajectory. If these non-decisional are independent from any decision-related dynamics, we can assess their joint influence by combining a simulated distribution generated by the embodied decision-making model with the observed distribution of baseline AUCs without a decision component.

Figure 4-9 illustrates this approach in generating a predicted distribution of AUCs in the hard-choice condition. For every simulated choice trial, we first randomly sample a baseline trial (with replacement). Then, given a set of model parameters, we simulate a reaching trajectory from the embodied decision model. The curvature of this simulated trajectory is simply added to that of the baseline trajectory. By repeating this procedure many times, we effectively combine the baseline AUC distribution with a predicted distribution of curvatures expected from the decision

model. Essentially, the question we now ask is what degree of curvature needs to be added to the basic curvature that we can already expect without a decision component, in order to account for the AUCs observed in the (hard) choice condition. In other words, the decision model now becomes responsible for modifying the baseline distribution in such a way as to account for the observed data in the hard-choice condition. For the example illustrated in Figure 4-9, we can see that adding the simulated distribution to the baseline distribution has two effects: it shifts the distribution of AUC values slightly to the right and increases the spread of the distribution, through a more pronounced right-hand skew.

Figure 4-9 Illustration of the effect of combining a simulated curvature distribution and a baseline

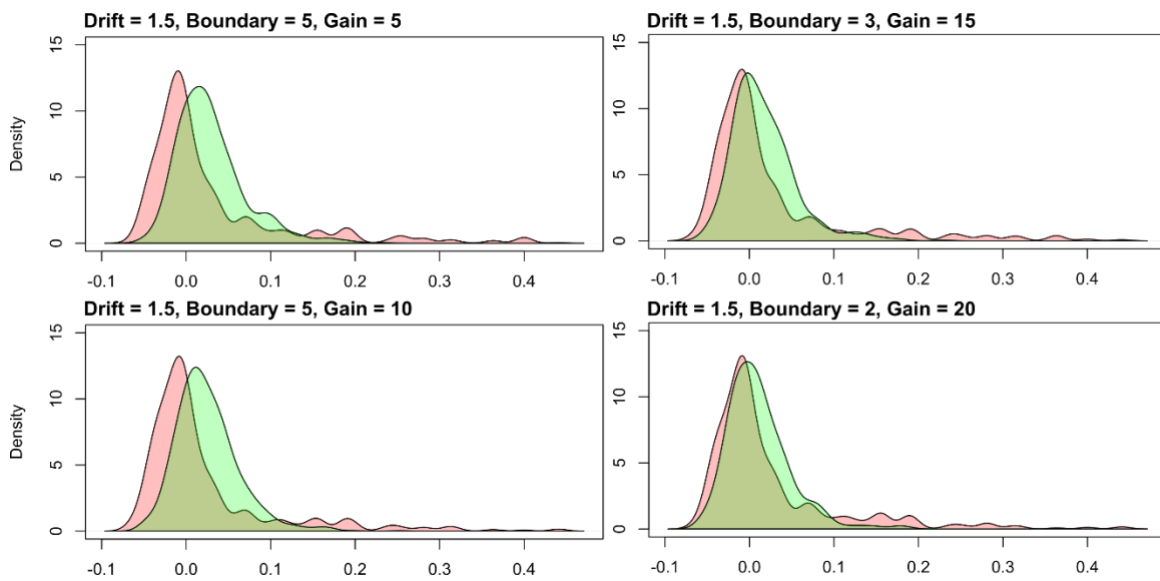


Note. The yellow curve is a kernel density plot of AUC values generated by a run of the trajectory simulation algorithm. The blue curve is the distribution of AUCs generated by a participant in the baseline no-choice condition. The green curve is the kernel density plot after these two distributions are convolved by adding random picks from the baseline AUC to the simulated AUCs.

The green distribution in Figure 4-9 may represent the imposition of some decision uncertainty on baseline trials where we assume there is none, which may allow the model to produce the kind of reach trajectories under greater perceptual uncertainty. For any participant in the study, we can now compare the empirically gathered distribution of trajectory curvatures in the hard condition with the combination of baseline and simulated curvatures. Using the parameter

exploration conducted earlier in this chapter we can see how different combinations of parameters modify the baseline distributions in such a way as to approximate the trajectories in the hard choice condition. Figure 4-10 illustrates this approach for participant four, using a number of different combinations of the boundary and gain values.

Figure 4-10 Four sets of baseline-modified simulated reach curvatures, with an empirical hard-choice distribution as comparison.



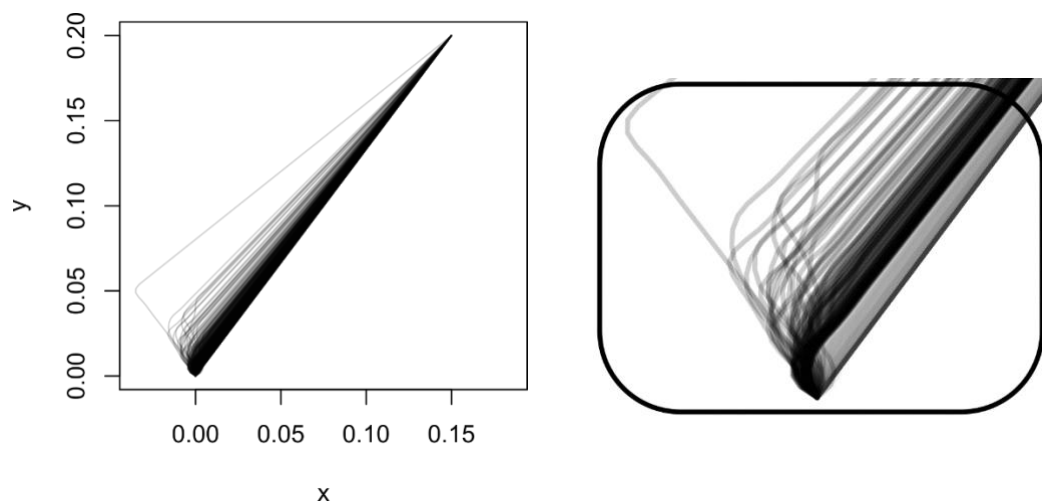
Note. Simulated curvature trajectory distributions are each the result of the continuous flow model, convolved with the baseline distribution for participant four.

While this is not an exhaustive search of the potential parameter space, some parameter values can get us close to approximating the empirical distribution from decision trials using the simulation method. For example, a drift parameter of 1.5, a boundary of 2 and a gain factor of 20 – a rather extreme set of parameters – appears to provide a more reasonable description of the AUC distribution from the choice trials (bottom right). Note that such close that drift and boundary parameters like these in a classical decide-then-act model would lead to very fast decisions. More generally, given the large degree of overlap between the baseline distribution and the distribution of AUCs in the hard choice condition, there actually is not much room for the decision model to approximate the curvatures in the choice condition when every baseline measurement is subjected to some degree of modification. As most of the change relative to the

baseline comes in the form of an elongated right-hand tail, while the largest component of the choice-condition remains close to zero, the best the decision model can do is take the baseline distribution and add a relatively small number of trials with large positive AUCs to them. For most trials, the decision model should leave the baseline data “untouched”. This kind of modification can only happen for a decision model that generates simulated trajectories that generally have an AUC close to 0, but with the occasional large positive curvature. The other parameter combinations shown in Figure 4-10 (top row and bottom left) all meet this criterion (see Figures 4-5 to 4-7), but even then do not provide a very good account of the empirical distribution from the hard condition, and maintaining a peak close to zero comes at the expense of the tail length. To get a better approximation, an even more extreme set of parameters had to be found (bottom right panel). This set of parameters predicts that the vast majority of reaches go straight to the target, but there are some a few change-of-mind trials that are responsible for elongating the right-hand tail of the distribution, as can be seen in

Figure 4-11.

Figure 4-11 Unmodified simulated trajectories, with a close-up of the start location



#### 4.6 *Alternative model formulation including variability in starting point*

The above model combined a drift-diffusion model of perceptual decision and reach generation by linking the reach heading to the state of an accumulating decision variable. The exploration so far have demonstrated that extreme parameter values are necessary to generate reach trajectories which resemble the experimental data, even after combining the baseline reach curvatures. Specifically, the drift rate needs to be high enough to reach a decision boundary quickly, and the boundary separation has to be narrow enough so that decision noise will move the decision variable below the alternative decision boundary in at least some of the trials. Here I will describe an alternative model which may generate more realistic trajectories.

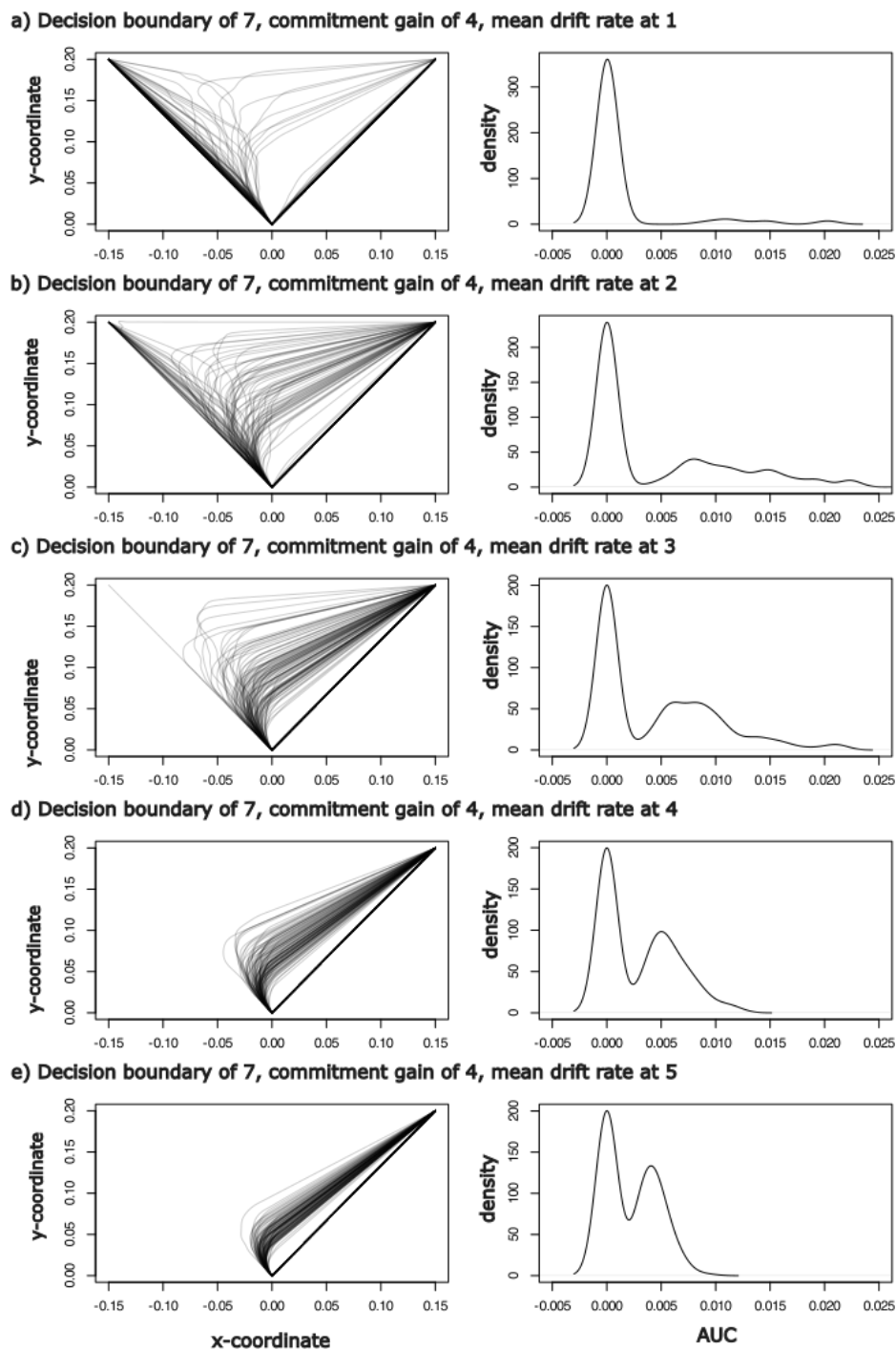
Rather than starting each random walk at zero, we can modify the starting value of the random walk to be identical to one of the two decision boundaries. If the starting value of the decision variable is the upper boundary, then the simulated effector will travel directly towards the correct target in the vast majority of simulated trials. If the starting value is the lower decision boundary, then the simulated effector will start travelling towards the incorrect target but shift to the correct target as evidence is accumulated. Noise in the accumulation process will spread out the simulated trajectories.

For each run of the simulation set of 200 random walks with a set drift rate and noise value were generated using the same custom functions as above. The value of the decision boundary was added to half of these random walks, and for the other half the value of the decision boundary was subtracted. The output of a selection of simulations is in Figure 4-12. The simulation parameters for decision boundary and commitment gain are set, and the mean drift rate is varied from a relatively low value (compared to the decision boundary) to a high value.

In all the simulations the random walks which start at the upper decision boundary terminate at the correct target location (top right of the coordinate plots). For the random walks which start at the lower decision boundary their likely termination location is modified by the drift rate

parameter. Low values of the drift rate parameter (the upper rows in Figure 4-12) cause most of the trials with an incorrect starting point to terminate at the incorrect target location, though there are some fluctuations in trajectory for the high-start random walks. High values of the drift rate parameter cause most of the initially incorrect trajectories to curve around to the correct target, but extinguish any fluctuation in the initially correct trials.

Figure 4-12 Trajectory simulations with starting points at the decision boundaries



Note. Each row presents the simulated trajectories based on 200 random walks. Half (100) of the random walks start at the lower decision boundary and the other half start at the upper decision boundary. The left column are the simulated trajectories, where trajectories terminating at the top-left are errors, and trajectories terminating at the top-right are correct. The right column of plots is the AUC distribution of correctly terminating reaches. Rows a to e increase the mean drift rate. The decision boundary and commitment gain values are fixed for all simulations.

The trajectory data presented in Chapter 3, from all participants, had the following relevant features: A substantial proportion of trials were initiated towards the right-hand target in left-target trials while only a small proportion of trials initiated towards the left hand target in right-target trials. Overall errors, i.e. trials where the incorrect target was retrieved, were rare but did happen occasionally. Finally, there was some remaining effect of trial difficulty after change of mind trials had been removed. No single value of the drift rate parameter can capture all the aforementioned features of the data at the same time. To allow overall reach errors to occur at all, and for there to be variability in curvature for correct reaches, the drift rate parameter needs to be low, but for most of the simulated reaches to be corrected the drift rate parameter needs to be high.

Modification of the decision boundary or commitment gain values are presented in Appendix C (Figure 0-1 and Figure 0-2) and follow a similar pattern. Narrow decision boundaries cause most trajectories generated from random walks with starting points at the lower boundary to curve back around to the correct target location, while wide decision boundaries allow too many simulated trajectories to terminate at the incorrect target location. Similarly, low levels of commitment gain (including zero) leads to all the trajectories curving back to the correct target location, and high levels of commitment gain lead to a large proportion of the simulated trajectories terminating at the incorrect target location.

This model is a pure change of mind model of trajectory generation which captures more of features of the experimental data but without the extreme parameter values needed for the model which starts with zero evidence. However it still does not match the curvature distributions from the experimental data. We can perform the same convolution with the baseline curvature distributions to account for biomechanical noise as above and see whether this generates a more realistic trajectory distribution. Furthermore we can take some of the characteristics of participant performance to help choose whether any trajectory generated

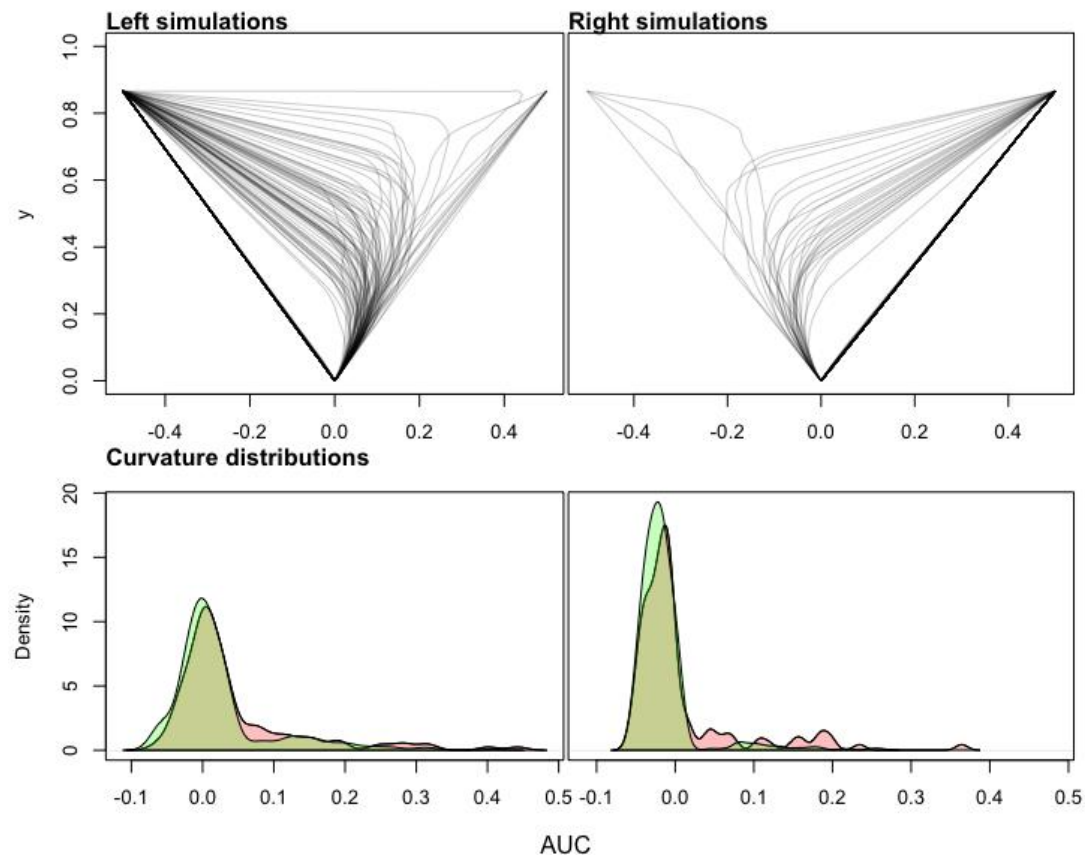


starts at the upper or lower boundary. Figure 4-13 was generated from 960 random walks, half are to targets on the left and half to right targets. The proportion on each side which start at the lower decision boundary (so that the initial reach direction is to the incorrect target) is based on the performance of participant 4, who initiated 146 out of 300 left-target trials to the right hand side, and 20 out of 298 right-target trials to the left hand side. The green curves on the bottom row plots represent the simulated AUCs convolved with the baseline curvature distribution for the respective side, and the red curves are the recorded AUC distributions for the hard choice condition, again separated by target side.

The simulated AUC distribution for right targets appears to replicate well the distribution gathered in the hard choice condition for participant 4. However there is less correspondence for the simulated reaches on the left-target reaches, with the bimodality inherent to a pure change of mind model surviving the convolution step. Equivalent plots for the other participants are in Appendix C (Figure 0-3 to Figure 0-7), and show a similar pattern of relatively good correspondence to the curvature distributions to right-hand targets, but correspond less often to the reaches to the left hand targets.

Overall this modification to the model, which builds-in changes of mind to a subset of trajectories based on the actual performance of the participants, still struggles to replicate the trajectory curvature distribution generated by the participants in the third experiment. Visual inspection of the simulated trajectories also indicate that, even with the commitment gain mechanism, the realism of the trajectories is still insufficient.

Figure 4-13 Simulated trajectories and curvature distributions for participant 4



Note. The top row are the simulated trajectories generated with a decision boundary of 9, a mean drift rate of 3 and a commitment gain parameter of 4; on the left panel of the top row 48% of the random walks start at the lower decision boundary and on the right panel 7% of the random walks start at the lower decision boundary. The bottom row presents kernel density plots of the simulated curvature values (in green) and the recorded curvature values from the hard choice condition of participant 4.

#### 4.7 Discussion

The aim of this chapter was to explore a process model linking the accumulation of evidence under perceptual uncertainty to reaching movement trajectories. The model embodies an assumption frequently encountered in the mouse tracking literature (with varying degrees of explicitness), namely that the decision variable in evidence accumulation models (such as the DDM), is translated into the heading of the effector due to competition between response options. The model involves a continuous flow between the decision variable and the reach target. The model was explored to assess whether and how it can generate trajectories like

those found empirically when participants are tasked to reach for one of two targets under conditions of perceptual uncertainty.

The model, taken from Lepora and Pezzulo (2015), translates a random walk into a trajectory, treating a decision as “made” when the effector reaches the target, rather than the internal decision variable simply crossing a decision boundary. The model starts the reach with the decision variable at zero and the focus point, towards which the effector is moved, directly between the target positions. At each time step, the decision variable is incremented according to the mean drift and noise parameters, and the focus point is updated to reflect this strength of evidence between the targets. After this calculation the effector is moved a set distance towards the focus point (i.e. at a constant velocity).

A random walk which quickly crosses the correct decision boundary will have a very direct path to the target and little curvature. Due to accumulation noise other paths are possible, including paths that show strong curvature toward the non-target, as reported in mouse tracking studies (Freeman, 2018). If an incorrect boundary is crossed early, the reach path will be directed towards the incorrect target with little curvature, with some chance of a correcting movement. If neither boundary is crossed the reach path will show a large curvature due spending most of the reach heading towards neither target, fluctuating between the two. This latter case is problematic as human movements do not show this kind of fluctuating behaviour. To smooth out these fluctuations a commitment effect was added to the model, on the principle that reaches during choice are in part informed by the current position of the hand itself. This commitment effect is implemented via feedback into the decision variable – essentially using the proximity of the effector to the target as evidence that the current reach target is appropriate. In terms of the trajectory curvature, this mechanism pulls the effector towards the nearer target, reducing late fluctuations in the reach path. Lepora and Pezzulo (2015) refer to this model as ‘embodied’, because the state of the effector is fed into the decision process.

The mapping between the random walk and the focus point, along with the commitment effect, changes how classical DDM parameters can be interpreted. Since the decision variable itself now incorporates information from the motor system (by using the commitment effect), the mean drift rate can still be interpreted as the perceptual quality of the evidence, but instantaneous value of the accumulator variable contains both perceptual and what we might call motor evidence. The accumulator crossing the decision boundary also no longer coincides with a finished decision process, but shows when there is confidence in the current target, at least temporarily.

This model has three parameters which influence the curvature of the reach: the mean drift rate of the decision variable, the boundary in the decision model, and the gain factor applied to the commitment effect. I explored whether and how these parameters, individually and in combination, allowed the model to generate curvature distributions like those found in hard decision trials from the experiments presented earlier. The *mean drift rate* determines the rate of evidence accumulation, and increasing this parameter has the effect of decreasing overall curvature of the reach paths. At higher values, the upper boundary for the (correct) decision is reached quickly, the reach path heads towards the target not long after the reach is initiated, and the distribution is narrow. At lower values, the decision process takes time to terminate, the reach path continues straight ahead for more of the reach, leading to increased curvature, and the distributions widens.

The decision boundary influences the reach paths in a complementary manner, with lower values leading to quicker decisions, and higher values leading to slower, and more curved paths. As the boundary increases the distribution widens slightly, but at very high values of the boundary parameter the distribution becomes narrower. The commitment gain, in contrast, exerts little influence at the start of the reach but increases in influence late in the reach. Increasing the commitment effect gain reduces curvature because it effectively strengthens the

evidence for the currently favoured target (analogous to a change in drift), while lower values allow a wider distribution of curvatures.

The purpose of the model is to simulate the reach-to-grasp path under perceptual decision-making and compare the simulated distributions to those from experimental work. The location and shape of the simulated distribution can be altered by changing the parameters in the model, and if a similar distribution to the empirical data can be achieved, those parameters can be informative about the underlying psychological processes. The empirical distributions of curvature from hard choice trials had a sharp peak and a long positive tail. The distributions from the easy conditions also had a sharp peak but a less pronounced tail.

#### 4.7.1 Biomechanical and non-decision influences on reach path

There are multiple combinations of parameter values that can lead to a distribution with a high peak and a long tail which may be similar in shape to that found in the empirical data. However, a notable feature of the empirical data was the position of the distribution: The mean signed curvature was close to zero or below zero indicating that most of the reaches are more-or-less direct, and frequently curve *away* from the competing target. This is behaviour that the continuous control model is unable to simulate. Other models of reaching and eye movement trajectories can account for curvature away from a non-target (Meeter et al., 2010; Tipper et al., 1994). These accounts rely on an inhibitory mechanism that acts on a (continuous) motor map, where the target and non-target are represented by overlapping populations of units. Inhibiting the non-target also ends up silencing some of the units involved in coding the target. When the movement is directed at the population average across the map, this inhibition drives the initial direction of the movement away from both the target and the non-target. Subsequent correction of this initial deviation then results in a trajectory that curves away from the non-target. For eye movements, several authors have shown that the direction of curvature depends on the movement latency (McSorley & McCloy, 2009; Van der Stigchel et al., 2006). Inhibition

takes time to develop, so curvature away from a non-target is only seen when the latency is sufficiently long. Systematic (negative) curvature away from a non-target is rarely reported in mouse tracking studies, though when raw trajectories are presented they can be seen (Kieslich et al., 2020). In many of these studies participants are encouraged (either explicitly or implicitly) to start moving as early as possible, which might explain why the typical direction of curvature is towards the non-target.

However, in the experiments presented here participants were also encouraged to start moving quickly. Moreover, in a “no decision” baseline control condition of Experiment 3 the mean curvature was also negative (relative to an empty non-target location), suggesting there are other factors that lead participants to curve reach paths away from the non-target. Observations from human motion literature (Corbetta & Santello, 2018; D’avella & Lacquaniti, 2013) suggest that there are biomechanical reasons that an optimal reach path between two points will not be direct: Depending on the starting position and the ending position, and the ease of moving the shoulder relative to the elbow joint, an energy efficient reach path may deviate from the ideal line. Before incorporating complex assumptions about time-varying inhibitory processes, it is necessary to explore whether and how a basic model that includes these other factors is able to account for the trajectory data in the hard choice condition.

One option to incorporate the biomechanical constraints that result in negative curvature would be to shift the simulated distribution of reaches by the mean baseline curvature. However, this solution would be incomplete because there is also significant variability in the baseline condition. By shifting the simulated distribution by a constant we are making the assumption that *all* of the variability, even in baseline trials, stemmed from the decision process. The baseline reaches also showed considerable variability in their trajectories. There are many degrees of freedom that can be minimised in terms of both muscle activation and reach path to achieve the goal. However, there are also other degrees of freedom in the movement which

have no influence on the speed, energy, or accuracy of the reach, and thus are not constrained, allowing a variety of movement paths to be energy efficient, quick and accurate (Martin et al., 2019). Moreover, other sources of noise such as noise in perceptual localisation or, indeed, noise in the initial motor command will also introduce variability in the trajectories even when there is target selection decision to be made (Shi & Buneo, 2012).

Therefore, the approach adopted here was to take the curvatures from the baseline condition as prototype curvatures upon which choice processes could be imposed. The trajectories observed in this condition are representative of the degree of curvature and its variability without the intervention of a decision process. In other words, the baseline distribution may be regarded as a statistical representation of all the non-decision related factors that influence the trajectory. The question then becomes how we can turn the baseline distribution of curvatures into the observed distribution of curvatures in the hard choice condition, through the assumptions of the embodied decision model.

To combine the baseline trials with the simulated decision process, a procedure was used which randomly sampled one baseline reach path and a simulated reach path and combined them. The resulting convolution of empirical baseline data and simulated data can be compared to the empirical trials when a decision is made. Parameter combinations from the earlier exploratory phase were used to see if any set of parameters in the model could approximate the empirical distributions.

Most combinations led to a modal value for the simulated reaches that was higher than that of the empirical decision trials, as shown in Figure 4-10. Setting parameters which tended to produce a longer tail of trials also moved the modal value further away from the empirical mode. To find a set of parameters which got close to the empirical data required a very low decision boundary, relative to the mean drift rate, and a high gain to limit any later changes. As a result of the low decision boundary, the action focus either very quickly settled on the target

favoured by evidence accumulation and only in rare cases did it lead towards the incorrect target before switching back, relatively early in the simulated reach, effectively forcing the model to simulate a change of mind process to generate trajectories, despite the random walks used as input strictly starting with zero evidence.

The model that included both non-decisional factors (represented by the baseline reaches) and an embodied decision process is only able to provide a reasonable descriptive account for the trajectories observed in the hard choice condition when extreme parameter values are chosen. The results of Chapter 3 showed that the hard choice distributions could be explained by a combination of an unmodified baseline distribution and an additional distribution. The decision process is primarily responsible for elongating the right-hand tail which includes reaches that curved strongly towards the non-target. Indeed, the closest model distribution involved combining the baseline distribution with a simulated distribution with a sharp peak near 0 and a long tail. The largest curvatures produced by the simulation model effectively represents a change-of-mind model.

Given that the assumptions of target blending and a strict continuous flow of decision information into that blend needed such extreme values to approximate the experimental data, a further modification to the model was implemented. Rather than starting with zero information, each random walk was started at one or other decision boundary. This corresponds to initiating a reach only after the decision process has already hit one absorbing boundary, much like the model of Resulaj et al. (2009). This modification allowed a somewhat more reasonable approximation of the experimental curvature distributions, particularly when the participant's own data were used to set how often the random walk started at the upper boundary (for a correct initial decision) or at the lower boundary (for an incorrect initial decision).



However, Lepora and Pezzulo (2015) claimed that a change-of-mind model was not a viable competitor for explaining mouse movement trajectories. It may have been that mouse movements are fundamentally different from the whole-arm reach-to-grasp movements under consideration here. However, the continuous flow with commitment model does not contain any biomechanical constraints or other forms of noise outside the decision process. While these limited assumptions may be sufficient to account for average mouse movement trajectories, it seems clear that they fall short in accounting for whole arm movement trajectories.

The Lepora and Pezzulo (2015) model required a commitment effect to generate realistic mouse-movement trajectories from mouse-tracking experiments by Barca and Pezzulo (2012) which showed apparently continuous revisions. However the trajectories that they were trying to replicate were from mouse-tracking experiments which required participants to start moving before the response options were revealed, however other research into intermediate reach trajectories from go-before-you-know paradigms indicate that participants reach forwards to a position between the response options, not because they have blended the action plans, but because they are merely hedging their bets (Haith et al, 2015). Similarly, intermediate trajectories from mouse tracking experiments are seen in more go-after-you-know tasks, but often only after trajectory averaging has been used on the data (Kieslich et al., 2020).

Furthermore, for 3D reaching data there is an additional consideration which may manifest as something like a commitment effect – the inertia of a moving arm. A mechanism, such as the commitment gain in the models above, may be necessary to simulate more realistic trajectories, but the underlying process may instead just be one which emerges from physical constraints (Wong, Cluff & Kuo, 2021).

Nevertheless, the exploration of the model here suggests that changes-of-mind, when combined with a statistical representation of non-decision factors may provide a reasonable account of the trajectories in the choice conditions. A mechanism for constructing curved trajectories using

through superimposing minimum jerk submovements, in a similar fashion to Friedman and colleagues (2013) or Henis and Flash (1995) may be able to generate smoothly curving trajectories which represent a pure change of mind model, but this would still need some way to incorporate motor variability. Future developments of this approach may improve the verisimilitude of process models which link decision-making processes and reach trajectories, however it seems unlikely that a strong version of continuous flow of information from perceptual systems to motor control is necessary for data like these.

#### *4.8 Conclusion*

In conclusion, the model that combined baseline variability with a continuous flow of decision-related activity into motor systems is somewhat unsatisfactory. While deviation towards the non-target is relatively rare in the empirical data, the inclusion of decision-related variability on all trials was unable to replicate the empirical findings without extreme parameter values. The strong influence of seemingly unmodified baseline trajectories in the choice trial conditions points to a model where only a subset of trials are executed with the influence of ongoing decisions. An extension of the model to start trials with a target already selected does better, but now requires changes of mind, and so cannot account for residual influences of trial difficulty observed in the experimental data even after change of mind trajectories had been removed.

## Chapter 5 General Discussion

This chapter recapitulated the aims and background of the thesis, summarises the main findings from the experimental and simulation work, and details the unique contribution of this thesis. A set of hypothetical models are outlined which may be more appropriate descriptions of the process leading from decision to action. Strengths and limitations of the work outlined in this thesis are evaluated, along with some potential future directions for this research topic.

## 5.1 *Aims of the thesis*

With the aim to explore the link between perceptual decision making and reaching behaviour, this thesis aimed to develop an experimental paradigm which could manipulate perceptual uncertainty in a way that could feed through to the motor control of a highly ecological act of reaching to grasp. The thesis introduced the concept of computational modelling and how it has been used to formalise explanations of human decision making performance, and how models of perceptual evidence accumulation in particular can explain the accuracy and latency of many decisions, not just those in the domain of perception (Ratcliff et al., 2016). The success of evidence accumulation models to explain decision making behaviour led on to neurophysiological studies which claimed to find neural correlates of the same processes (Gold & Shadlen, 2007). These studies often concluded that the neural activity which implements evidence accumulation could happen in areas of the brain related to the motor response to a task, rather than only in areas of the brain typically assigned a notion of abstract “executive” functioning (Pastor-Bernier & Cisek, 2011). Based on these kinds of results, it was suggested the act of choosing is as much a process of competition between motor actions than weighing up the utility of one course of action over another (Cisek, 2007).

This turn is related to the idea of “embodied cognition”, which suggests that in real behaviour the processes of perceiving, deciding and acting are dynamically intertwined in a way that traditional psychological research is ill-equipped to study (Gordon et al., 2021). Rather than treating cognitive processing as a series of discrete processing stages, where it is only the fully resolved results of some computation which are passed on to the next cognitive module, information continuously flows into an organism and ongoing behaviour is dynamically adjusted in response (Spivey, 2008; Spivey & Dale, 2004, 2006). Such continuities can therefore be leveraged by research psychologists to investigate the dynamics of cognitive processes with

process tracing techniques, including that of mouse tracking (Freeman, 2018; Koop & Johnson, 2011; Schulte-Mecklenbeck et al., 2017; Song & Nakayama, 2009).

At the extreme end of this point of view, the concept of what it means to “make a decision” needs to be re-evaluated: Is it when we begin an action, or when we complete it? If we have only “made” a decision once it has been completed, then the trajectories of reaching with a hand or a computer mouse computer mice really are readouts of ongoing decisional processing (Lepora & Pezzulo, 2015). Inspired by this kind of work, I conducted a number of experiments into how reach to grasp actions change, or not, when enacted under conditions of increased perceptual uncertainty. Furthermore, I examined whether a frequently cited model of continuous information flow from perception to action could be scaled up to a more “naturalistic” reach to grasp action, over and above the kinds of trajectories frequently recorded in mouse tracking research and explored an extension to the model which may better account for the behavioural data gathered. To summarise, this thesis addresses the following questions: (i) how does perceptual uncertainty influence reach to grasp actions; and (ii) how may the link between an evidence accumulation process and reach paths be modelled?

## *5.2 Summary of main findings*

To address these questions an experimental paradigm was developed to manipulate perceptual uncertainty while participants performed rapid reach to grasp actions. Unlike most research which has investigated this topic, the information on which to base decisions about the reach goal was to be gathered from the potential targets themselves. During the experiment two pairs of reach objects were used as stimuli, the easy choice pair had a large difference in luminance, and the hard choice pair a close difference in luminance. Participants were seated, but otherwise unconstrained, with their hand placed at a starting location which meant that to pick up either block the reach had to travel an equal distance forward and left or forwards and right. Before each trial participants were told to pick up either the lighter or darker of the targets and to be as

fast and as accurate as possible, but not whether the trial was in the easy or hard condition. Trials began when a liquid crystal screen turned from opaque to clear with no other warning tone or cue. The trial ended two seconds after the trial began. Motion capture data was processed to extract the movement initiation time, the grasp time and the curvature of the reach path.

This main finding of these experiments was that increasing perceptual uncertainty does, indeed, influence the reach to grasp action. In experiment 1 from Chapter 2, higher perceptual uncertainty increased overall reach times, initiation times, movement times and induced more “attraction” to the non-target, indexed as more positive average reach path curvature in trials when there was a lower difference in the luminance of the targets. To introduce another source of uncertainty into the task, experiment 2 implemented a feedback mechanism to the participant to encourage rapid movement initiation within 400ms of the trial start. With this addition the influence of perceptual difficulty on initiation times was reduced, but not eliminated. Nor did an analysis of either experiment with “change of mind” trials removed indicate that change of mind trajectories were the sole source of a shift in overall curvature for the hard choice trials when compared with the easy choice trials. The conclusion provided by these experiments was that choice processes influence reach to grasp actions in the following ways: Reaches to grasp do not default to a strictly serial decide-then-act process of decision making and action. Furthermore, the influence of target uncertainty is not always limited to trials where there is an initial error which is later corrected, referred to in this thesis as a change of mind. This finding counts against explanations which suggest that increased path deviation is due solely to the revision of action initiation mistakes, or uninformed guesses. Notably, it was also observed that the location and orientation of the target had a consistent influence on reach timing and curvature, and that further investigation of this problem needed to take this into account. Beyond the curvature of the reach to grasp path, the experiments manipulated the orientation of the targets to be retrieved with the aim of investigating grasp shaping as well as

reach path, however the variability inherent to motor actions meant that potential signals of delayed grasp shaping were not evident in the collected data.

Chapter 3 reported the results and analysis of the third experiment. This experiment replicated the method of experiment 2 with two important modifications. Baseline trials, where only one target was present so that no choice was required, were intermixed into the experiment and fewer participants completed many more trials. The target orientation manipulations were retained to allow a comparison of results between the second and third experiments. A comparison of the easy choice trials and the hard choice trials replicated the results of Chapter 2, and a supplementary analysis found that the participants frequently made initial reaches to the right hand target regardless of trial difficulty, particularly for very rapidly initiated reaches. A unique contribution of chapter 3 was a distributional analysis of the reach trajectories recorded in the choice conditions. Hypothesising that the baseline trials reflect behaviour without any choice processes or perceptual uncertainty, the distribution curvatures in baseline trials for each target side were fit with an ex-Gaussian distribution. I then explored a number of modifications of this baseline distribution in an effort to identify what parameters of the baseline distribution need to change in order to accommodate the choice condition curvature distributions. Rather than a single parameter modification of the distributions, the best fitting models for choice condition data were most often weighted mixture of two ex-Gaussian distributions: one with the same parameters as the baseline, and an additional distribution with a different set of parameters. The distribution with the baseline parameters represented the majority of reaches in choice trials which were as direct to be indistinguishable from the no-choice trials. The additional distribution typically modelled an extra population of reaches with an overall higher curvature (towards the non-target) than those of the baseline distribution, but often overlapped with the baseline distribution and were predominantly exponential in shape. These distributions did not only capture “change of mind” trajectories, but also other which blended into the range of the baseline distribution. The conclusion of this chapter was that the biomechanical

constraints on reach paths and the influence of motor noise are major sources of variability in reach paths where there is no decision to be made. Any process model that links decision making processes to reach paths must accommodate this variability, as well as multiple overlapping populations of reach curvatures.

Chapter 4 of this thesis developed a model to link the state of a decision variable with the path taken during reaching movements. It was a modification of the “embodied choice” model presented in Lepora and Pezzulo (2015) which claimed to replicate mouse paths recorded for a study into lexical decision making. The model supposes that the instantaneous heading of a reach action is the average of movement plans for each potential target, weighted by the state of the decision variable at the time, and that target selection occurs during the reach, with the balance of evidence (from a drift diffusion model) wetting the weighting between target representations. The model may be thought of as ‘embodied’ because a feedback mechanism biases the decision variable towards the target that is closest to the effector. This mechanism smooths out trajectories that would otherwise fluctuate along with the noisiness of the evidence accumulator. To accommodate the inherent noisiness captured by the baseline trials in experiment 3, the Lepora and Pezzulo model was set up with information about the mean speed and geometry of the workspace. The reach path curvatures generated by the model were added to empirical baseline curvatures, and the resulting distributions examined for resemblance to the distribution choice trials.

Most importantly, the way the model was used to link evidence accumulation and reach curvature only captures the *additional* variability imposed by choice processes. Following the results of chapter three, a model needs to large curvatures values to a small proportion of trials, and little to no curvature to the remaining trials. Therefore, the curvature distribution produced by the model needs a sharp peak at zero curvature, and an elongated tail. The only way to achieve this sharp peak is to set the value of the decision boundary very low, so that the “action



focus” of the simulated reach settles on the final target very soon into any trial. Rare large curvatures were generated by random walks which crossed the lower boundary instead, settling the “action focus” on the incorrect option until evidence had accumulated back up to the upper decision boundary. The stochastic component of the model could no longer be said to be one of dynamic accumulation of evidence towards a decision, but instead one that predominantly switches between the options – a model which changes its mind.

The model was developed further by setting the starting values for the random walks at the decision boundaries. The proportion of direct trials to change of mind trials was used from the behavioural data to set how often each random walk started at either the upper or lower decision boundary. This turned the model into one that could *only* generate either direct trials or change-of-mind trials. When convolved with the baseline reach variability from the behavioural data, curvature distributions similar to the behavioural data were generated, however the model could no longer account for shifts in curvature which were observed in the behavioural data.

To summarise, increasing the perceptual uncertainty of participants asked to make rapid reach to grasp movement increased the incidence and extent of path deviations towards the non-target, an increase which cannot be explained as due only to an increase in changes of mind. For reaches to single targets there is a large amount of variance in reach curvature due to motor noise and biomechanical constraints on reach paths. A continuous flow model of the link between decision accumulation and reach path generation struggled to generate reach path distributions similar to those recorded in hard-choice conditions. Incorporating the baseline curvatures to account for the variance seen in the absence of choice brought the simulated trajectories *closer* to the observed trajectories, but not to a satisfying degree. Setting simulation parameters so that large near zero curvatures could be generated also caused the decision component to behave more like a system which changes its mind, rather than one in which information (and uncertainty) flows into motor control. Setting simulation parameters so that

reaches are initiated with a target already in mind were more successful at generating realistic curvature distributions.

### 5.3 *Interpretation in context of literature*

This thesis suggested several ways to model the link between evidence accumulation and the generation of reach paths. It must be noted that for unconstrained reach-to-grasp actions such as these, the variability of reach paths even in the baseline trials, presented an interesting challenge. Whatever the contribution of perceptual decision making to reach to grasp actions, the biomechanical constraints on the reach-to-grasp path will add a systematic bias to the reach curvature, and any motor noise in execution may have increased the variance of these reach trajectories independently of decision processes (van Beers et al., 2004).

A long-standing issue in the field of human motor control is the “degrees of freedom problem” (Bernstein, 1967). To briefly illustrate this, consider that you can use the muscles in your upper arm to move your elbow either inwards or outwards; it has one degree of freedom. However, there are many joints involved in whole arm reaching and the degrees of freedom of each joint combined together means that to move your hand from one location to another there are infinitely many paths your hand can take, and an infinite number of ways to configure your shoulder and arm to trace the same hand path. Recent work in human motor control has suggested that movement variability may be optimised to achieve goals efficiently and flexibly, and it follows from this that the motor system needs only to control the degrees of freedom that may adversely impact overall performance (Latash et al., 2002, 2007). Variability which does not adversely affect overall task performance is not controlled (Martin et al., 2019). For example, a slight error in launch trajectory to either the left or right can be rectified with a later corrective movement to the right or left, and since the two paths are energetically and temporally equivalent sacrificing speed for accuracy has no more benefit (Trommershäuser et al., 2005). It is on this kind of motor control system that decision processes will interact with movement.

Of the potential links between decision processes and stereotypical reach generation the simplest model, where decisions were entirely resolved before movements were initiated, is clearly unable to explain the data from experiment 1. The most complex model, where decision making processes exert continuous control of reaching actions, is also unsatisfactory, at least for the instantiation developed in chapter 4 (the Lepora and Pezzulo model augmented with baseline variability). An extension to the model which explicitly engineers a change of mind process is better at simulating the behavioural data, but not completely.

The remaining models are those where ongoing control is possible but intermittently applied. There are thresholds between decision making processes and movements associated with those processes. Of these there were three distinct flavours: Change of mind models (Resulaj et al., 2009), motor averaging of sub-movement models (Friedman et al., 2013), and performance optimisation models (Wong & Haith, 2017).

It is possible that reach paths recorded in this paradigm really were the result of a “pure change of mind” link between decision making and action, despite the influence of difficulty remaining in some measures after change of mind trials were identified and removed from the mixed model analysis in Chapters 2 and 3. Under such a model there is no continuous flow of information from perceptual systems into motor systems, and if there is a process of evidence accumulation to a threshold it will trigger movement preparation and initiation in a very similar fashion to older decision models (Atiya et al., 2020; Cos et al., 2021b; Kiani et al., 2014; Resulaj et al., 2009; van den Berg et al., 2016). To accommodate potential changes of mind these models allow accumulation processes to continue; the movement goal is revised if another decision boundary is crossed in time. Thus, there is no access for the movement system to any dynamics emanating from decision systems, there is either no available goal, because no decision boundary has yet been crossed, or the current goal switches from one target to another.

A slight add-on to the pure change of mind system could accommodate the remaining effect of trial difficulty in direct trials. If a covert target switch happens just before reach initiation and averaged movement trajectories are generated as in Henis and Flash (1995), the reach target may not have been sufficiently suppressed. Recall that when Henis and Flash switched targets sufficiently early in the movement preparation phase the first reach target was internally shifted to an intermediate position. The final curved movement was a superposition of a minimum-jerk trajectory to the intermediate position and the minimum-jerk trajectory from the intermediate position to the final position. For this experiment, therefore, the reach paths recorded may have been a mixture of the following trajectory types: direct reaches with no internal target switch, reaches with an internal target switch after movement initiation or too late in movement preparation to prevent a change of mind, and reaches with an internal target switch early in movement preparation which resulted in a mixing of trajectories and a curved reaching path. Note that this scheme does not require a continuous flow of decision information into motor systems. The decision is not “made” via motor plan selection as stronger versions of embodied cognition theories suggest. Some kind of trajectory averaging may be produced, and motor plans do interfere with each other, but this is not a process which is tightly integrated with the perceptual decision itself.

There is an alternative explanation for the curved reaching path that does not depend on motor averaging at all. There may only ever be one motor plan active if target selection had not finished and the goal was still uncertain (Wong et al., 2015). Instead of mixing motor plans together, the optimal policy is to deploy a motor plan to minimise potential costs for switching targets. Direct reaching movements in a go-before-you-know task were observed by Wong and Haith (2017) when participants were required to reach rapidly to one of two potential targets, but when instructed to slow down their reaching movements many more intermediate reach paths were recorded. Furthermore these intermediate trajectories can be biased by the participant’s awareness of the likely final target location (Hudson et al., 2007). In this experiment

target information was available before reach initiation, so when firm evidence for target selection is unavailable at the time of reach initiation, an intermediate solution may have been deployed until the real target is identified. For the easier trials the optimised motor plan will have been revised earlier, reducing apparent overall attraction to the non-target when trial information was aggregated, and these intermediate headings may also be themselves adjusted according to participant estimates of the probable target location for the upcoming trial.

Alternatively, there may be some access to the state of the decision variable at reach initiation, even if no evidence threshold has yet been crossed. This formulation is that of the intermittent control of submovements model (Friedman et al., 2013). Recall that this model suggested multiple interacting decision processes: one “timing” accumulator to launch the initial reach, and another accumulator to gather evidence on which select the target. For the data from these experiments the target decision process may often have been completely resolved on or before reach initiation. Should the timing accumulator hit threshold before the decision accumulator, the latter is interrogated and a reach is prepared and executed such that its heading is towards an intermediate location and its amplitude is such that an expected correction can smoothly divert the reach once decision processes sufficiently resolve. It is plausible that this is close to the process implemented by participants to perform well at this task, particularly in experiments 2 and 3 where there was external feedback to incentivise early reach initiation. As participants adapted to the task, internal parameters for both the timing and decision accumulators were adjusted to meet the initiation deadline requirement while maintaining overall success rates.

The first and third models above can be placed into a dynamic field theory framework of movement preparation and execution (Erlhagen & Schöner, 2002), which informed the development of the embodied cognition framework (Cisek, 2007). Dynamic Field Theory suggests that at the neural level decisions continuously evolve, and hallmarks of this continuity is expressed in the curvature of executed movement paths. Before any trial begins, a participant

will have multiple candidate motor plans prepared, two if it is only the reach to the target location which is coded for, or four if it is the reach and grasp for each potential target. Each of these motor plans are represented by a pattern of ongoing, noisy, neural activity. At the start of a trial perceptual evidence will flow towards this activity, strengthening the activity of the motor plan for reaching to grasp the preferred target. Once activity for one of the motor plans reaches a threshold, that movement is triggered. This framework also allows for the activity of motor plans at the start of the trial to already show some difference in activation levels, either due to random noise or expectations or predictions that the participant may have for the upcoming trial. This last point may also be able to explain the rare baseline trials which also seemed to diverge strongly from the typical reach path. While no alternative target was available visible in these trials, the no-choice, easy choice and hard choice trials were presented to participants in a random order, so motor plan activity towards non-existent targets may have been particularly active just before these trials.

#### *5.4 Contribution of the work*

A strong thread in the critiques of “classic” cognitive science by the proponents of embodied cognition is that lab-based reaction time experiments impose a somewhat artificial constraint on the kinds of theories that can be generated from such experiments (Garbarini & Adenzato, 2004). This work takes those criticisms seriously, and presents results from a series of experiments where the stimuli are not a random dot kinematogram but real objects, the movement is not restricted to the plane by either a robot arm (Cos et al., 2021b; Resulaj et al., 2009) or the requirement to push a computer mouse (Freeman, 2018) but instead free to move in three dimensions, nor is the information on which to select a target withheld from the participants before they start their movements and fully revealed after movement initiation.

The linear mixed model approach used in this thesis compared performance measures between easy- and hard-choice trials for all experiments allowed a careful analysis of the distribution of

these measures without aggregating across trials. In combination with this analytical approach, the distribution fitting approach taken in Chapter 3 identified that much of the variation seen in reach movements under choice is also present when there is no choice to be made at all. The modelling work in Chapter 4 explicitly tested the linking assumptions between decision making and movement paths of an influential model of mouse tracking trajectories (Lepora & Pezzulo, 2015). Overall, this work has narrowed down the space of possible models that can link decision making to real movement generation.

Beyond these recommendations, it can also be suggested that the model suggested by Lepora and Pezzulo (2015) is not particularly suited to generating realistic reaching trajectories. The mechanisms underlying both decision making and movement control may be “dynamic”, but this does not automatically translate into the kind of continuous control model that allows conclusions about cognitive processing to be drawn directly reach paths. Any viable model to link decision making processes to the generation reaching movements must have certain critical features: (i) an ability to generate typical reach paths and the variability of those reach paths when there is no target conflict; (ii) some variety of thresholding between decision processes and either movement planning or execution; and (iii) a mechanism for triggering responses without a fully resolved decision. The development of the model to include starting point variability and so explicitly generat either direct or change of mind trajectories, however it seems clear that the noise in an evidence accumulation process is far from the most important source of variability in reach trajectories. Even if there is continuous flow of information from decision making into motor preparation areas as suggested by dynamic field theory, this does not survive into effects detectable at the trial level.

## 5.5 *Limitations*

This thesis has some methodological and analytical limitations which may have affected the conclusions. Foremost, the unfruitful inclusion of target orientation as an independent variable

increased variability in the reach paths, particularly just before the moment of grasp. The statistical analysis approach (linear mixed modelling) will have been able to account for this in the analyses conducted on all trials, however the step of removing changes of mind will have unbalanced the data somewhat. That said, the distributional analysis in Chapter 3, which found good fits of the hard-choice data from a mixture of the baseline and an often overlapping additional distribution back up the conclusions from the mixed model analyses. The procedure to identify a change of mind would also have influenced the conclusions. For this thesis a conservative criterion was chosen where any deviation towards the non-target in the early part of the reach was regarded as a change of mind. This may have identified trajectories where a participant's lift-off deviated slightly to one side when in fact no change of mind had happened at all. In some cases the 10Hz low-pass filter would have smoothed out these deviations, but in cases where it may not have, a more relaxed change of mind criterion will only have reduced the sensitivity of the procedure to detect higher AUC values driven by increased choice difficulty. It's possible that other choices of a cut off frequency to filter the raw trajectories before analysis will have changed the precise moment that a reach initiation or grasp moment was recorded, however (as visible in Appendix B) the important features of each reach and retrieve trajectory will not be shifted a great deal – the variability of reach initiation or of grasp time across trials was much greater than any inaccuracies from trajectory filtering.

The proponents of embodied cognition may still criticise the paradigm presented in this thesis as continuing the contrived classical approach to the psychology of decision making (Gordon et al., 2021). The choice presented in these studies is still a discrete one, with a correct and an incorrect option at each trial, while embodiment theorists emphasise the continuity between the value of potential actions (Yoo et al., 2021). Exemplifying this problem, the perceptual decision in these experiments was a judgement about the relative luminance of objects. Previous work either used random dot kinematograms (RDKs) as the source of perceptual evidence (e.g. Friedman et al., 2013; Resulaj et al., 2009), or highly complex stimuli which are



chosen for their ambiguity (Schneider et al., 2015), require linguistic processing (eg. Spivey et al., 2005), social cognitive processing (eg. Stillman et al., 2018), or multiple attributes to be evaluated at once (Ha et al., 2016). Furthermore, RDKs have been extensively leveraged in decision making research because it takes time to integrate motion evidence before coming to a decision (Ratcliff et al., 2016) and the very noisiness of the stimulus may be a better stand in for a tricky judgement. Relatedly the judgements required for studies into higher level cognitive processing often require extended periods of deliberation. As such the contrast judgement used here may just be too straightforward to require an equivalent accumulative decision process to the RDK. However the main aim of this thesis was to contribute to knowledge about the relationship between basic perceptual decisions and motor behaviour, and this has been achieved.

Another key feature of “embodied decisions” is that they are explicitly about deciding-while-acting, instead of deciding-then-acting (Gordon et al., 2021). In the language of mouse-tracking research this experiment used a more-or-less “static” starting procedure, rather than a “dynamic” one (Grage et al., 2019; Kieslich et al., 2020). A static starting procedure allows participants to view the stimuli before initiating movement, while dynamic starting procedures require participants to start moving before the stimuli are shown, much like the go-before-you-know tasks used in the investigations into motor control (Chapman et al., 2010; Gallivan et al., 2017, 2018; Wispinski et al., 2020), or a lion selecting which prey animal from the herd to chase down (Cisek, 1999, 2007; Gordon et al., 2021). If ongoing movements are a window into the dynamics of decision making (Maldonado et al., 2019), a static starting procedure allows decisions to be resolved covertly, closing that window.

A change to how the decision process in these experiments is modelled may be warranted to improve the simulation of reach paths. The drift diffusion model of decision making is only one of a large number of potential decision making mechanisms (Evans & Wagenmakers, 2020). One

often used alternative to the drift diffusion model is the linear ballistic accumulator model (LBA; Brown & Heathcote, 2008). Rather than a two-sided diffusion accumulator for the binary choice process, separate LBAs can be used to model response time for each stimulus, and a further one for timing a strategic intermediate response (Hawkins & Heathcote, 2021). A simulation using LBAs as the decision input may be able to generate either version of the change of mind model. A version which launches a reach based on the decision accumulator when the timing accumulator finishes will implement a version of the intermittent control model by Friedman and colleagues (2013). On the other hand if the reach is not launched with any information, the model will reflect the assumptions underlying the performance optimisation approach by Wong and Haith (2017). It should be noted that the study by Friedman and colleagues (2013) presented and compared a pair of models similar to the intermittent control model with partial information and the intermittent control model with no information at reach launch. They concluded that the partial information model fit their data better, but did not compare their model against a model which allowed participants to make a guess at a likely, or easy, target location and then revise that decision.

## *5.6 Future Directions*

Based on the findings in this thesis further work on the link between perceptual decision making and reach to grasp actions should look beyond the continuous flow model. Continuous flow may work for some varieties of go-before-you-know paradigms, but real reaching to real objects is rarely so constrained. Future experiments where only target location is varied will provide better estimates of a participant's sensitivity to trial difficulty effects. On the modelling side, an approach using LBA modelling, such as in Hawkins & Heathcote (2021), along with a system to generate biomechanically realistic trajectories could narrow down the threshold between direct movements and curved movements.

## 5.7 *Overall Conclusion*

This thesis started with a discussion of the information processing account of decision and action and contrasted it with the embodied cognition approach. A series of experiments which aimed to be slightly more ecologically valid than the usual tasks used in decision making research were carried out. Participants made real judgements about real objects and grasped them with their real hands, and a model was developed to explore the linkage between these processes. In conclusion, this research into the link between perceptual decision making and reach to grasp action has shown that the tight link between

## References

- Alhussein, L., & Smith, M. A. (2021). Motor planning under uncertainty. *ELife*, *10*, e67019.  
<https://doi.org/10.7554/eLife.67019>
- Anders, R., Riès, S., van Maanen, L., & Alario, F.-X. (2015). Evidence accumulation as a model for lexical selection. *Cognitive Psychology*, *82*, 57–73.  
<https://doi.org/10.1016/j.cogpsych.2015.07.002>
- Anzola, G. P., Bertoloni, G., Buchtel, H. A., & Rizzolatti, G. (1977). Spatial compatibility and anatomical factors in simple and choice reaction time. *Neuropsychologia*, *15*(2), 295–302. [https://doi.org/10.1016/0028-3932\(77\)90038-0](https://doi.org/10.1016/0028-3932(77)90038-0)
- Arbib, M. A., & Bonaiuto, J. J. (Eds.). (2016). *From neuron to cognition via computational neuroscience*. The MIT Press.
- Atiya, N. A. A., Zgonnikov, A., O’Hora, D., Schoemann, M., Scherbaum, S., & Wong-Lin, K. (2020). Changes-of-mind in the absence of new post-decision evidence. *PLOS Computational Biology*, *16*(2), e1007149. <https://doi.org/10.1371/journal.pcbi.1007149>
- Audley, R. J. (1960). A stochastic model for individual choice behavior. *Psychological Review*, *67*, 1–15. <https://doi.org/10.1037/h0046438>
- Barca, L., & Pezzulo, G. (2012). Unfolding Visual Lexical Decision in Time. *PLOS ONE*, *7*(4), e35932. <https://doi.org/10.1371/journal.pone.0035932>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1), Article 1.  
<https://doi.org/10.18637/jss.v067.i01>
- Bates, D., Maechler, M., Bolker, [aut, B., cre, Walker, S., Christensen, R. H. B., Singmann, H., Dai, B., Scheipl, F., Grothendieck, G., Green, P., Fox, J., Bauer, A., & simulate.formula), P. N. K. (shared copyright on. (2021). *lme4: Linear Mixed-Effects Models using ‘Eigen’ and S4* (1.1-27.1) [Computer software]. <https://CRAN.R-project.org/package=lme4>

- Berlucchi, G., Heron, W., Hyman, R., Rizzolatti, G., & Umiltà, C. (1971). Simple reaction times of ipsilateral and contralateral hand to a lateralized visual stimuli. *Brain: A Journal of Neurology*, 94(3), 419–430. <https://doi.org/10.1093/brain/94.3.419>
- Bernstein, N. (1967). *Coordinate and Regulation of Movements*. Pergamon P.
- Bleser, G., Damen, D., Behera, A., Hendebby, G., Mura, K., Miezal, M., Gee, A., Petersen, N., Mações, G., Domingues, H., Gorecky, D., Almeida, L., Mayol-Cuevas, W., Calway, A., Cohn, A. G., Hogg, D. C., & Stricker, D. (2015). Cognitive Learning, Monitoring and Assistance of Industrial Workflows Using Egocentric Sensor Networks. *PLOS ONE*, 10(6), e0127769. <https://doi.org/10.1371/journal.pone.0127769>
- Bogacz, R., Brown, E., Moehlis, J., Holmes, P., & Cohen, J. D. (2006). The physics of optimal decision making: A formal analysis of models of performance in two-alternative forced-choice tasks. *Psychological Review*, 113(4), 700–765. <https://doi.org/10.1037/0033-295x.113.4.700>
- Brette, R. (2022). Brains as Computers: Metaphor, Analogy, Theory or Fact? *Frontiers in Ecology and Evolution*, 10. <https://www.frontiersin.org/articles/10.3389/fevo.2022.878729>
- Britten, K. H., Shadlen, M. N., Newsome, W. T., & Movshon, J. A. (1992). The analysis of visual motion: A comparison of neuronal and psychophysical performance. *Journal of Neuroscience*, 12(12), 4745–4765. <https://doi.org/10.1523/JNEUROSCI.12-12-04745.1992>
- Brown, S. D., & Heathcote, A. (2008). The simplest complete model of choice response time: Linear ballistic accumulation. *Cognitive Psychology*, 57(3), 153–178. <https://doi.org/10.1016/j.cogpsych.2007.12.002>
- Bundt, C., Ruitenberg, M. F. L., Abrahamse, E. L., & Notebaert, W. (2018). Early and late indications of item-specific control in a Stroop mouse tracking study. *PLOS ONE*, 13(5), e0197278. <https://doi.org/10.1371/journal.pone.0197278>

- Carnahan, H., Goodale, M. A., & Marteniuk, R. G. (1993). Grasping versus pointing and the differential use of visual feedback. *Human Movement Science*, 12(3), 219–234.  
[https://doi.org/10.1016/0167-9457\(93\)90016-I](https://doi.org/10.1016/0167-9457(93)90016-I)
- Cartwright, D., & Festinger, L. (1943). A quantitative theory of decision. *Psychological Review*, 50(6), 595–621. <https://doi.org/10.1037/h0056982>
- Chapman, C. S., Gallivan, J. P., Wood, D. K., Milne, J. L., Culham, J. C., & Goodale, M. A. (2010). Reaching for the unknown: Multiple target encoding and real-time decision-making in a rapid reach task. *Cognition*, 116(2), 168–176.  
<https://doi.org/10.1016/j.cognition.2010.04.008>
- Churchland, A. K., Kiani, R., & Shadlen, M. N. (2008). Decision-making with multiple alternatives. *Nature Neuroscience*, 11(6), 693–702. <https://doi.org/10.1038/nn.2123>
- Cisek, P. (1999). Beyond the computer metaphor: Behaviour as interaction. *Journal of Consciousness Studies*, 6(11–12), 125–142.
- Cisek, P. (2007). Cortical mechanisms of action selection: The affordance competition hypothesis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362(1485), 1585–1599. <https://doi.org/10.1098/rstb.2007.2054>
- Cisek, P. (2012). Making decisions through a distributed consensus. *Current Opinion in Neurobiology*, 22(6), 927–936. <https://doi.org/10.1016/j.conb.2012.05.007>
- Cisek, P., & Kalaska, J. F. (2005). Neural correlates of reaching decisions in dorsal premotor cortex: Specification of multiple direction choices and final selection of action. *Neuron*, 45(5), 801–814. <https://doi.org/10.1016/j.neuron.2005.01.027>
- Cisek, P., & Kalaska, J. F. (2010). Neural Mechanisms for Interacting with a World Full of Action Choices. *Annual Review of Neuroscience*, 33(1), 269–298.  
<https://doi.org/10.1146/annurev.neuro.051508.135409>
- Clark, A. (1999). An embodied cognitive science? *Trends in Cognitive Sciences*, 3(9), 345–351.  
[https://doi.org/10.1016/S1364-6613\(99\)01361-3](https://doi.org/10.1016/S1364-6613(99)01361-3)

- Corbetta, D., & Santello, M. (Eds.). (2018). *Reach-to-grasp behavior: Brain, behavior and modelling across the life span*. Routledge.
- Cos, I., Bélanger, N., & Cisek, P. (2011). The influence of predicted arm biomechanics on decision making. *Journal of Neurophysiology*, *105*(6), 3022–3033.  
<https://doi.org/10.1152/jn.00975.2010>
- Cos, I., Pezzulo, G., & Cisek, P. (2021a). Changes of mind after movement onset: A motor-state dependent decision-making process. *BioRxiv*, 2021.02.15.431196.  
<https://doi.org/10.1101/2021.02.15.431196>
- Cos, I., Pezzulo, G., & Cisek, P. (2021b). Changes of Mind after Movement Onset Depend on the State of the Motor System. *ENeuro*, *8*(6). <https://doi.org/10.1523/ENEURO.0174-21.2021>
- Dale, R., Kehoe, C., & Spivey, M. J. (2007). Graded motor responses in the time course of categorizing atypical exemplars. *Memory & Cognition*, *35*(1), 15–28.  
<https://doi.org/10.3758/BF03195938>
- D'avella, A., & Lacquaniti, F. (2013). Control of reaching movements by muscle synergy combinations. *Frontiers in Computational Neuroscience*, *7*, 42.  
<https://doi.org/10.3389/fncom.2013.00042>
- De Comite, A., Crevecoeur, F., & Lefèvre, P. (2021). Online modification of goal-directed control in human reaching movements. *Journal of Neurophysiology*, *125*(5), 1883–1898.  
<https://doi.org/10.1152/jn.00536.2020>
- Dekleva, B. M., Kording, K. P., & Miller, L. E. (2018). Single reach plans in dorsal premotor cortex during a two-target task. *Nature Communications*, *9*(1), 3556.  
<https://doi.org/10.1038/s41467-018-05959-y>
- Diedrichsen, J., Shadmehr, R., & Ivry, R. B. (2010). The coordination of movement: Optimal feedback control and beyond. *Trends in Cognitive Sciences*, *14*(1), 31–39.  
<https://doi.org/10.1016/j.tics.2009.11.004>

- Dotan, D., Pinheiro-Chagas, P., Al Roumi, F., & Dehaene, S. (2019). Track It to Crack It: Dissecting Processing Stages with Finger Tracking. *Trends in Cognitive Sciences*, 23(12), 1058–1070.  
<https://doi.org/10.1016/j.tics.2019.10.002>
- Enachescu, V., Schrater, P., Schaal, S., & Christopoulos, V. (2021). Action planning and control under uncertainty emerge through a desirability-driven competition between parallel encoding motor plans. *PLOS Computational Biology*, 17(10), e1009429.  
<https://doi.org/10.1371/journal.pcbi.1009429>
- Erlhagen, W., & Schöner, G. (2002). Dynamic field theory of movement preparation. *Psychological Review*, 109(3), 545–572. <https://doi.org/10.1037/0033-295X.109.3.545>
- Evans, N. J., & Wagenmakers, E.-J. (2020). Evidence Accumulation Models: Current Limitations and Future Directions. In *The Quantitative Methods for Psychology* (Vol. 16, Issue 2, pp. 73–90). <https://doi.org/10.20982/tqmp.16.2.p073>
- Fabbri, S., Strnad, L., Caramazza, A., & Lingnau, A. (2014). Overlapping representations for grip type and reach direction. *NeuroImage*, 94, 138–146.  
<https://doi.org/10.1016/j.neuroimage.2014.03.017>
- Faulkenberry, T. J., Witte, M., & Hartmann, M. (2018). *Tracking the continuous dynamics of numerical processing: A brief review and editorial*.  
<https://doi.org/10.23668/psycharchives.1494>
- Fischer, M. H., & Hartmann, M. (2014). Pushing forward in embodied cognition: May we mouse the mathematical mind? *Frontiers in Psychology*, 5.  
<https://doi.org/10.3389/fpsyg.2014.01315>
- Fitts, P. M. (1954). The information capacity of the human motor system in controlling the amplitude of movement. *Journal of Experimental Psychology*, 47(6), 381–391.  
<https://doi.org/10.1037/h0055392>



- Flanagan, J. R., & Lolley, S. (2001). The Inertial Anisotropy of the Arm Is Accurately Predicted during Movement Planning. *Journal of Neuroscience*, 21(4), 1361–1369.  
<https://doi.org/10.1523/JNEUROSCI.21-04-01361.2001>
- Flash, T., & Henis, E. (1991). Arm Trajectory Modifications During Reaching Towards Visual Targets. *Journal of Cognitive Neuroscience*, 3(3), 220–230.  
<https://doi.org/10.1162/jocn.1991.3.3.220>
- Flash, T., & Hogan, N. (1985). The coordination of arm movements: An experimentally confirmed mathematical model. *Journal of Neuroscience*, 5(7), 1688–1703.
- Freeman, J. B. (2018). Doing Psychological Science by Hand. *Current Directions in Psychological Science*, 27(5), 315–323. <https://doi.org/10.1177/0963721417746793>
- Freeman, J. B., & Ambady, N. (2010). MouseTracker: Software for studying real-time mental processing using a computer mouse-tracking method. *Behavior Research Methods*, 42(1), 226–241. <https://doi.org/10.3758/BRM.42.1.226>
- Freeman, J. B., Ambady, N., Rule, N. O., & Johnson, K. L. (2008). Will a category cue attract you? Motor output reveals dynamic competition across person construal. *Journal of Experimental Psychology: General*, 137(4), 673–690. <https://doi.org/10.1037/a0013875>
- Freeman, J. B., & Dale, R. (2013). Assessing bimodality to detect the presence of a dual cognitive process. *Behavior Research Methods*, 45(1), 83–97. <https://doi.org/10.3758/s13428-012-0225-x>
- Friedman, J., Brown, S., & Finkbeiner, M. (2013). Linking cognitive and reaching trajectories via intermittent movement control. *Journal of Mathematical Psychology*, 57(3–4), 140–151.  
<https://doi.org/10.1016/j.jmp.2013.06.005>
- Friedman, J., & Korman, M. (2012). Kinematic Strategies Underlying Improvement in the Acquisition of a Sequential Finger Task with Self-Generated vs. Cued Repetition Training. *PLOS ONE*, 7(12), e52063. <https://doi.org/10.1371/journal.pone.0052063>

- Friston, K. (2011). What Is Optimal about Motor Control? *Neuron*, 72(3), 488–498.  
<https://doi.org/10.1016/j.neuron.2011.10.018>
- Gallivan, J. P., Barton, K. S., Chapman, C. S., Wolpert, D. M., & Flanagan, J. R. (2015). Action plan co-optimization reveals the parallel encoding of competing reach movements. *Nature Communications*, 6, 7428. <https://doi.org/10.1038/ncomms8428>
- Gallivan, J. P., & Chapman, C. S. (2014). Three-dimensional reach trajectories as a probe of real-time decision-making between multiple competing targets. *Frontiers in Neuroscience*, 8, 215. <https://doi.org/10.3389/fnins.2014.00215>
- Gallivan, J. P., Chapman, C. S., Wolpert, D. M., & Flanagan, J. R. (2018). Decision-making in sensorimotor control. *Nature Reviews Neuroscience*, 19(9), Article 9.  
<https://doi.org/10.1038/s41583-018-0045-9>
- Gallivan, J. P., Stewart, B. M., Baugh, L. A., Wolpert, D. M., & Flanagan, J. R. (2017). Rapid Automatic Motor Encoding of Competing Reach Options. *Cell Reports*, 18(7), 1619–1626.  
<https://doi.org/10.1016/j.celrep.2017.01.049>
- Garbarini, F., & Adenzato, M. (2004). At the root of embodied cognition: Cognitive science meets neurophysiology. *Brain and Cognition*, 56(1), 100–106.  
<https://doi.org/10.1016/j.bandc.2004.06.003>
- Gawthrop, P., Loram, I., Lakie, M., & Gollee, H. (2011). Intermittent control: A computational theory of human control. *Biological Cybernetics*, 104(1), 31–51.  
<https://doi.org/10.1007/s00422-010-0416-4>
- Gentilucci, M., Castiello, U., Corradini, M. L., Scarpa, M., Umiltà, C., & Rizzolatti, G. (1991). Influence of different types of grasping on the transport component of prehension movements. *Neuropsychologia*, 29(5), 361–378. [https://doi.org/10.1016/0028-3932\(91\)90025-4](https://doi.org/10.1016/0028-3932(91)90025-4)
- Georgii, C., Schulte-Mecklenbeck, M., Richard, A., Van Dyck, Z., & Blechert, J. (2020). The dynamics of self-control: Within-participant modeling of binary food choices and

- underlying decision processes as a function of restrained eating. *Psychological Research*, 84(7), 1777–1788. <https://doi.org/10.1007/s00426-019-01185-3>
- Georgopoulos, A. P. (1990). Neurophysiology of reaching. In *Attention and performance 13: Motor representation and control* (pp. 227–263). Lawrence Erlbaum Associates, Inc.
- Georgopoulos, A. P., Schwartz, A. B., & Kettner, R. E. (1986). Neuronal Population Coding of Movement Direction. *Science*, 233(4771), 1416–1419. <https://doi.org/10.1126/science.3749885>
- Gibson, J. J. (1986). *The Ecological Approach To Visual Perception*. Psychology Press. <https://doi.org/10.4324/9780203767764>
- Gold, J. I., & Shadlen, M. N. (2007). The Neural Basis of Decision Making. *Annual Review of Neuroscience*, 30(1), 535–574. <https://doi.org/10.1146/annurev.neuro.29.051605.113038>
- Gordon, J., Maselli, A., Lancia, G. L., Thiery, T., Cisek, P., & Pezzulo, G. (2021). The road towards understanding embodied decisions. *Neuroscience & Biobehavioral Reviews*, 131, 722–736. <https://doi.org/10.1016/j.neubiorev.2021.09.034>
- Grage, T., Schoemann, M., Kieslich, P. J., & Scherbaum, S. (2019). Lost to translation: How design factors of the mouse-tracking procedure impact the inference from action to cognition. *Attention, Perception, & Psychophysics*, 81(7), 2538–2557. <https://doi.org/10.3758/s13414-019-01889-z>
- Griffith, T., Baker, S.-A., & Lepora, N. F. (2021). The statistics of optimal decision making: Exploring the relationship between signal detection theory and sequential analysis. *Journal of Mathematical Psychology*, 103, 102544. <https://doi.org/10.1016/j.jmp.2021.102544>
- Gross, J., Timmermann, L., Kujala, J., Dirks, M., Schmitz, F., Salmelin, R., & Schnitzler, A. (2002). The neural basis of intermittent motor control in humans. *Proceedings of the National Academy of Sciences*, 99(4), 2299–2302. <https://doi.org/10.1073/pnas.032682099>

- Guigon, E., Baraduc, P., & Desmurget, M. (2008). Optimality, stochasticity, and variability in motor behavior. *Journal of Computational Neuroscience*, 24(1), 57–68.  
<https://doi.org/10.1007/s10827-007-0041-y>
- Ha, O.-R., Bruce, A. S., Pruitt, S. W., Cherry, J. B. C., Smith, T. R., Burkart, D., Bruce, J. M., & Lim, S.-L. (2016). Healthy eating decisions require efficient dietary self-control in children: A mouse-tracking food decision study. *Appetite*, 105, 575–581.  
<https://doi.org/10.1016/j.appet.2016.06.027>
- Haith, A. M., Huberdeau, D. M., & Krakauer, J. W. (2015). Hedging Your Bets: Intermediate Movements as Optimal Behavior in the Context of an Incomplete Decision. *PLOS Computational Biology*, 11(3), e1004171. <https://doi.org/10.1371/journal.pcbi.1004171>
- Hanes, D. P., & Schall, J. D. (1996). Neural Control of Voluntary Movement Initiation. *Science*.  
<https://doi.org/10.1126/science.274.5286.427>
- Harris, C. M., & Wolpert, D. M. (1998). Signal-dependent noise determines motor planning. *Nature*, 394(6695), 780–784. <https://doi.org/10.1038/29528>
- Harrison, X. A., Donaldson, L., Correa-Cano, M. E., Evans, J., Fisher, D. N., Goodwin, C. E. D., Robinson, B. S., Hodgson, D. J., & Inger, R. (2018). A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ*, 6, e4794.  
<https://doi.org/10.7717/peerj.4794>
- Hawkins, G. E., & Heathcote, A. (2021). Racing against the clock: Evidence-based versus time-based decisions. *Psychological Review*, 128(2), 222–263.  
<https://doi.org/10.1037/rev0000259>
- Heekeren, H. R., Marrett, S., Bandettini, P. A., & Ungerleider, L. G. (2004). A general mechanism for perceptual decision-making in the human brain. *Nature*, 431(7010), 859–862.  
<https://doi.org/10.1038/nature02966>

- Heekeren, H. R., Marrett, S., & Ungerleider, L. G. (2008). The neural systems that mediate human perceptual decision making. *Nature Reviews Neuroscience*, 9(6), 467–479.  
<https://doi.org/10.1038/nrn2374>
- Heft, H. (1989). Affordances and the body: An intentional analysis of Gibson's ecological approach to visual perception. *Journal for the Theory of Social Behaviour*, 19, 1–30.  
<https://doi.org/10.1111/j.1468-5914.1989.tb00133.x>
- Heitz, R. P. (2014). The speed-accuracy tradeoff: History, physiology, methodology, and behavior. *Frontiers in Neuroscience*, 8.  
<https://www.frontiersin.org/article/10.3389/fnins.2014.00150>
- Henis, E. A., & Flash, T. (1995). Mechanisms underlying the generation of averaged modified trajectories. *Biological Cybernetics*, 72(5), 407–419.  
<https://doi.org/10.1007/BF00201416>
- Henmon, V. A. C. (1911). The relation of the time of a judgment to its accuracy. *Psychological Review*, 18(3), 186–201. <https://doi.org/10.1037/h0074579>
- Heras-Escribano, M. (2021). Pragmatism, enactivism, and ecological psychology: Towards a unified approach to post-cognitivism. *Synthese*, 198(1), 337–363.  
<https://doi.org/10.1007/s11229-019-02111-1>
- Ho, T. C., Brown, S., & Serences, J. T. (2009). Domain General Mechanisms of Perceptual Decision Making in Human Cortex. *Journal of Neuroscience*, 29(27), 8675–8687.  
<https://doi.org/10.1523/JNEUROSCI.5984-08.2009>
- Hudson, T. E., Maloney, L. T., & Landy, M. S. (2007). Movement Planning With Probabilistic Target Information. *Journal of Neurophysiology*, 98(5), 3034–3046.  
<https://doi.org/10.1152/jn.00858.2007>
- Hurley, S. (2001). Perception And Action: Alternative Views. *Synthese*, 129(1), 3–40.  
<https://doi.org/10.1023/A:1012643006930>

- Incera, S., & McLennan, C. T. (2018). Bilingualism and age are continuous variables that influence executive function. *Aging, Neuropsychology, and Cognition*, 25(3), 443–463.  
<https://doi.org/10.1080/13825585.2017.1319902>
- Jeannerod, M. (1988). *The neural and behavioural organization of goal-directed movements* (pp. xii, 283). Clarendon Press/Oxford University Press.
- Kahneman, D. (2013). *Thinking, fast and slow* (1st pbk. ed). Farrar, Straus and Giroux.
- Karl, J., & Whishaw, I. (2013). Different Evolutionary Origins for the Reach and the Grasp: An Explanation for Dual Visuomotor Channels in Primate Parietofrontal Cortex. *Frontiers in Neurology*, 4, 208. <https://doi.org/10.3389/fneur.2013.00208>
- Kelly, S. P., & O’Connell, R. G. (2015). The neural processes underlying perceptual decision making in humans: Recent progress and future directions. *Journal of Physiology-Paris*, 109(1), 27–37. <https://doi.org/10.1016/j.jphysparis.2014.08.003>
- Kiani, R., Cueva, C. J., Reppas, J. B., & Newsome, W. T. (2014). Dynamics of Neural Population Responses in Prefrontal Cortex Indicate Changes of Mind on Single Trials. *Current Biology*, 24(13), 1542–1547. <https://doi.org/10.1016/j.cub.2014.05.049>
- Kieslich, P. J., Schoemann, M., Grage, T., Hepp, J., & Scherbaum, S. (2020). Design factors in mouse-tracking: What makes a difference? *Behavior Research Methods*, 52(1), 317–341.  
<https://doi.org/10.3758/s13428-019-01228-y>
- Kim, H. E., Avraham, G., & Ivry, R. B. (2021). The Psychology of Reaching: Action Selection, Movement Implementation, and Sensorimotor Learning. *Annual Review of Psychology*, 72(1), 61–95. <https://doi.org/10.1146/annurev-psych-010419-051053>
- Kimura, T., & Nakano, W. (2021). Motor adaptation is promoted by an incongruent Stroop task, but not by a congruent Stroop task. *Experimental Brain Research*, 239(4), 1295–1303.  
<https://doi.org/10.1007/s00221-021-06059-y>

- Klein Breteler, M. D., Meulenbroek, R. G. J., & Gielen, S. C. A. M. (2002). An evaluation of the minimum-jerk and minimum torque-change principles at the path, trajectory, and movement-cost levels. *Motor Control*, 6(1), 69–83. <https://doi.org/10.1123/mcj.6.1.69>
- Knips, G., Zibner, S. K. U., Reimann, H., & Schöner, G. (2017). A Neural Dynamic Architecture for Reaching and Grasping Integrates Perception and Movement Generation and Enables On-Line Updating. *Frontiers in Neurorobotics*, 11. <https://www.frontiersin.org/articles/10.3389/fnbot.2017.00009>
- Koop, G. J., & Johnson, J. G. (2011). Response dynamics: A new window on the decision process. *Judgment and Decision Making*, 6(8), 750–758.
- Krajbich, I., Hare, T., Bartling, B., Morishima, Y., & Fehr, E. (2015). A Common Mechanism Underlying Food Choice and Social Decisions. *PLOS Computational Biology*, 11(10), e1004371. <https://doi.org/10.1371/journal.pcbi.1004371>
- Krüger, M., Straube, A., & Eggert, T. (2017). The Propagation of Movement Variability in Time: A Methodological Approach for Discrete Movements with Multiple Degrees of Freedom. *Frontiers in Computational Neuroscience*, 11, 93. <https://doi.org/10.3389/fncom.2017.00093>
- Kuznetsova, A., Brockhoff, P. B., Christensen, R. H. B., & Jensen, S. P. (2020). *lmerTest: Tests in Linear Mixed Effects Models* (3.1-3) [Computer software]. <https://CRAN.R-project.org/package=lmerTest>
- Lacquaniti, F., & Soechting, J. F. (1982). Coordination of arm and wrist motion during a reaching task. *Journal of Neuroscience*, 2(4), 399–408. <https://doi.org/10.1523/JNEUROSCI.02-04-00399.1982>
- Laird, J. E., Lebiere, C., & Rosenbloom, P. S. (2017). A Standard Model of the Mind: Toward a Common Computational Framework across Artificial Intelligence, Cognitive Science, Neuroscience, and Robotics. *AI Magazine*, 38(4), Article 4. <https://doi.org/10.1609/aimag.v38i4.2744>

- Latash, M. L. (2012). The bliss (not the problem) of motor abundance (not redundancy). *Experimental Brain Research*, 217(1), 1–5. <https://doi.org/10.1007/s00221-012-3000-4>
- Latash, M. L., Levin, M. F., Scholz, J. P., & Schöner, G. (2010). Motor control theories and their applications. *Medicina*, 46(6), Article 6. <https://doi.org/10.3390/medicina46060054>
- Latash, M. L., Scholz, J. P., & Schöner, G. (2002). Motor Control Strategies Revealed in the Structure of Motor Variability. *Exercise and Sport Sciences Reviews*, 30(1), 26–31.
- Latash, M. L., Scholz, J. P., & Schöner, G. (2007). Toward a new theory of motor synergies. *Motor Control*, 11(3), 276–308. <https://doi.org/10.1123/mcj.11.3.276>
- Leite, F. P., & Ratcliff, R. (2011). What cognitive processes drive response biases? A diffusion model analysis. *Judgment and Decision Making*, 6(7), 651–687.
- Lepora, N. F., & Pezzulo, G. (2015). Embodied Choice: How Action Influences Perceptual Decision Making. *PLOS Computational Biology*, 11(4), e1004110. <https://doi.org/10.1371/journal.pcbi.1004110>
- Lerche, V., & Voss, A. (2016). Model Complexity in Diffusion Modeling: Benefits of Making the Model More Parsimonious. *Frontiers in Psychology*, 7. <https://www.frontiersin.org/article/10.3389/fpsyg.2016.01324>
- Liao, J. Y., & Kirsch, R. F. (2014). Characterizing and Predicting Submovements during Human Three-Dimensional Arm Reaches. *PLOS ONE*, 9(7), e103387. <https://doi.org/10.1371/journal.pone.0103387>
- Lopez, R. B., Stillman, P. E., Heatherton, T. F., & Freeman, J. B. (2018). Minding One's Reach (To Eat): The Promise of Computer Mouse-Tracking to Study Self-Regulation of Eating. *Frontiers in Nutrition*, 0. <https://doi.org/10.3389/fnut.2018.00043>
- Loram, I. D., Gawthrop, P. J., & Lakie, M. (2006). The frequency of human, manual adjustments in balancing an inverted pendulum is constrained by intrinsic physiological factors. *The Journal of Physiology*, 577(Pt 1), 417–432. <https://doi.org/10.1113/jphysiol.2006.118786>



- Lu, C., & Proctor, R. W. (1995). The influence of irrelevant location information on performance: A review of the Simon and spatial Stroop effects. *Psychonomic Bulletin & Review*, 2(2), 174–207. <https://doi.org/10.3758/BF03210959>
- Maldonado, M., Dunbar, E., & Chemla, E. (2019). Mouse tracking as a window into decision making. *Behavior Research Methods*, 51(3), 1085–1101. <https://doi.org/10.3758/s13428-018-01194-x>
- Marghetis, T., Núñez, R., & Bergen, B. K. (2014). Doing arithmetic by hand: Hand movements during exact arithmetic reveal systematic, dynamic spatial processing. *The Quarterly Journal of Experimental Psychology*, 67(8), 1579–1596. <https://doi.org/10.1080/17470218.2014.897359>
- Marr, D., & Poggio, T. (1976). *From Understanding Computation to Understanding Neural Circuitry*. <https://dspace.mit.edu/handle/1721.1/5782>
- Martin, V., Reimann, H., & Schöner, G. (2019). A process account of the uncontrolled manifold structure of joint space variance in pointing movements. *Biological Cybernetics*, 113(3), 293–307. <https://doi.org/10.1007/s00422-019-00794-w>
- Mazurek, M. E., Roitman, J. D., Ditterich, J., & Shadlen, M. N. (2003). A Role for Neural Integrators in Perceptual Decision Making. *Cerebral Cortex*, 13(11), 1257–1269. <https://doi.org/10.1093/cercor/bhg097>
- Mazza, C., Monaro, M., Burla, F., Colasanti, M., Orrù, G., Ferracuti, S., & Roma, P. (2020). Use of mouse-tracking software to detect faking-good behavior on personality questionnaires: An explorative study. *Scientific Reports*, 10(1), 4835. <https://doi.org/10.1038/s41598-020-61636-5>
- McKinstry, C., Dale, R., & Spivey, M. J. (2008). Action Dynamics Reveal Parallel Competition in Decision Making. *Psychological Science*, 19(1), 22–24. <https://doi.org/10.1111/j.1467-9280.2008.02041.x>

- McSorley, E., & McCloy, R. (2009). Saccadic eye movements as an index of perceptual decision-making. *Experimental Brain Research*, 198(4), 513–520. <https://doi.org/10.1007/s00221-009-1952-9>
- Meeter, M., Van der Stigchel, S., & Theeuwes, J. (2010). A competitive integration model of exogenous and endogenous eye movements. *Biological Cybernetics*, 102(4), 271–291. <https://doi.org/10.1007/s00422-010-0365-y>
- Melnikoff, D. E., Mann, T. C., Stillman, P. E., Shen, X., & Ferguson, M. J. (2021). Tracking Prejudice: A Mouse-Tracking Measure of Evaluative Conflict Predicts Discriminatory Behavior. *Social Psychological and Personality Science*, 12(2), 266–272. <https://doi.org/10.1177/1948550619900574>
- Merel, J., Botvinick, M., & Wayne, G. (2019). Hierarchical motor control in mammals and machines. *Nature Communications*, 10(1), Article 1. <https://doi.org/10.1038/s41467-019-13239-6>
- Meteyard, L., & Davies, R. A. I. (2020). Best practice guidance for linear mixed-effects models in psychological science. *Journal of Memory and Language*, 112, 104092. <https://doi.org/10.1016/j.jml.2020.104092>
- Miklósi, Á., & Soproni, K. (2006). A comparative analysis of animals' understanding of the human pointing gesture. *Animal Cognition*, 9(2), 81–93. <https://doi.org/10.1007/s10071-005-0008-1>
- Milner, T. E., & Ijaz, M. M. (1990). The effect of accuracy constraints on three-dimensional movement kinematics. *Neuroscience*, 35(2), 365–374. [https://doi.org/10.1016/0306-4522\(90\)90090-Q](https://doi.org/10.1016/0306-4522(90)90090-Q)
- Moeller, K., Fischer, M. H., Nuerk, H.-C., & Willmes, K. (2009). Sequential or parallel decomposed processing of two-digit numbers? Evidence from eye-tracking. *Quarterly Journal of Experimental Psychology*, 62(2), 323–334. <https://doi.org/10.1080/17470210801946740>

- Moher, J., & Song, J.-H. (2019). A comparison of simple movement behaviors across three different devices. *Attention, Perception, & Psychophysics*, 81(7), 2558–2569.  
<https://doi.org/10.3758/s13414-019-01856-8>
- Monaro, M., Gamberini, L., & Sartori, G. (2017). The detection of faked identity using unexpected questions and mouse dynamics. *PLOS ONE*, 12(5), e0177851.  
<https://doi.org/10.1371/journal.pone.0177851>
- Morasso, P. (1981). Spatial control of arm movements. *Experimental Brain Research*, 42(2), 223–227. <https://doi.org/10.1007/BF00236911>
- Muenzinger, K. F. (1938). Vicarious Trial and Error at a Point of Choice: I. A General Survey of its Relation to Learning Efficiency. *The Pedagogical Seminary and Journal of Genetic Psychology*, 53(1), 75–86. <https://doi.org/10.1080/08856559.1938.10533799>
- Muenzinger, K. F., & Gentry, E. (1931). Tone discrimination in white rats. *Journal of Comparative Psychology*, 12(2), 195–206. <https://doi.org/10.1037/h0072238>
- Mulder, M. J., Wagenmakers, E.-J., Ratcliff, R., Boekel, W., & Forstmann, B. U. (2012). Bias in the Brain: A Diffusion Model Analysis of Prior Probability and Potential Payoff. *Journal of Neuroscience*, 32(7), 2335–2343. <https://doi.org/10.1523/JNEUROSCI.4156-11.2012>
- Nash, J. C., Varadhan, R., & Grothendieck, G. (2021). *optimx: Expanded Replacement and Extension of the 'optim' Function* (Version 2021-10.12) [Computer software].  
<https://CRAN.R-project.org/package=optimx>
- Nashed, J. Y., Crevecoeur, F., & Scott, S. H. (2014). Rapid Online Selection between Multiple Motor Plans. *Journal of Neuroscience*, 34(5), 1769–1780.  
<https://doi.org/10.1523/JNEUROSCI.3063-13.2014>
- Newsome, W. T., Britten, K. H., & Movshon, J. A. (1989). Neuronal correlates of a perceptual decision. *Nature*, 341(6237), 52–54. <https://doi.org/10.1038/341052a0>

- O'Connell, R. G., & Kelly, S. P. (2021). Neurophysiology of Human Perceptual Decision-Making. *Annual Review of Neuroscience*, 44(1), 495–516. <https://doi.org/10.1146/annurev-neuro-092019-100200>
- Ollman, R. (1966). Fast guesses in choice reaction time. *Psychonomic Science*, 6(4), 155–156. <https://doi.org/10.3758/BF03328004>
- Pastor-Bernier, A., & Cisek, P. (2011). Neural Correlates of Biased Competition in Premotor Cortex. *Journal of Neuroscience*, 31(19), 7083–7088. <https://doi.org/10.1523/JNEUROSCI.5681-10.2011>
- Paulignan, Y., MacKenzie, C., Marteniuk, R., & Jeannerod, M. (1991). Selective perturbation of visual input during prehension movements. *Experimental Brain Research*, 83(3), 502–512. <https://doi.org/10.1007/BF00229827>
- Pearce, A. L., Adise, S., Roberts, N. J., White, C., Geier, C. F., & Keller, K. L. (2020). Individual differences in the influence of taste and health impact successful dietary self-control: A mouse tracking food choice study in children. *Physiology & Behavior*, 223, 112990. <https://doi.org/10.1016/j.physbeh.2020.112990>
- Pezzulo, G., & Ognibene, D. (2012). Proactive Action Preparation: Seeing Action Preparation as a Continuous and Proactive Process. *Motor Control*, 16(3), 386–424. <https://doi.org/10.1123/mcj.16.3.386>
- Philiastides, M. G., Heekeren, H. R., & Sajda, P. (2014). Human Scalp Potentials Reflect a Mixture of Decision-Related Signals during Perceptual Choices. *Journal of Neuroscience*, 34(50), 16877–16889. <https://doi.org/10.1523/JNEUROSCI.3012-14.2014>
- Phillips, J. G., & Triggs, T. J. (2001). Characteristics of cursor trajectories controlled by the computer mouse. *Ergonomics*, 44(5), 527–536. <https://doi.org/10.1080/00140130121560>

- Pleskac, T. J., Cesario, J., & Johnson, D. J. (2018). How race affects evidence accumulation during the decision to shoot. *Psychonomic Bulletin & Review*, 25(4), 1301–1330.  
<https://doi.org/10.3758/s13423-017-1369-6>
- Purcell, B. A., & Palmeri, T. J. (2017). Relating accumulator model parameters and neural dynamics. *Journal of Mathematical Psychology*, 76, 156–171.  
<https://doi.org/10.1016/j.jmp.2016.07.001>
- R Core Team. (YEAR). *R: A language and environment for statistical computing* [Manual].  
<https://www.R-project.org>
- Radwin, R. G., Vanderheiden, G. C., & Lin, M.-L. (1990). A Method for Evaluating Head-Controlled Computer Input Devices Using Fitts' Law. *Human Factors*, 32(4), 423–438.  
<https://doi.org/10.1177/001872089003200405>
- Ratcliff, R. (1978). A theory of memory retrieval. *Psychological Review*, 85(2), 59–108.  
<https://doi.org/10.1037/0033-295X.85.2.59>
- Ratcliff, R., Hasegawa, Y. T., Hasegawa, R. P., Smith, P. L., & Segraves, M. A. (2007). Dual Diffusion Model for Single-Cell Recording Data From the Superior Colliculus in a Brightness-Discrimination Task. *Journal of Neurophysiology*, 97(2), 1756–1774.  
<https://doi.org/10.1152/jn.00393.2006>
- Ratcliff, R., & McKoon, G. (2008). The Diffusion Decision Model: Theory and Data for Two-Choice Decision Tasks. *Neural Computation*, 20(4), 873–922.  
<https://doi.org/10.1162/neco.2008.12-06-420>
- Ratcliff, R., Smith, P. L., Brown, S. D., & McKoon, G. (2016). Diffusion Decision Model: Current Issues and History. *Trends in Cognitive Sciences*, 20(4), 260–281.  
<https://doi.org/10.1016/j.tics.2016.01.007>
- Ratcliff, R., & Tuerlinckx, F. (2002). Estimating parameters of the diffusion model: Approaches to dealing with contaminant reaction times and parameter variability. *Psychonomic Bulletin & Review*, 9(3), 438–481. <https://doi.org/10.3758/BF03196302>

- Read, R. (2008). The 'Hard' Problem of Consciousness Is Continually Reproduced and Made Harder by All Attempts to Solve It. *Theory, Culture & Society*, 25(2), 51–86.  
<https://doi.org/10.1177/0263276407086791>
- Resulaj, A., Kiani, R., Wolpert, D. M., & Shadlen, M. N. (2009). Changes of mind in decision-making. *Nature*, 461(7261), Article 7261. <https://doi.org/10.1038/nature08275>
- Richert, M., Albright, T. D., & Krekelberg, B. (2013). The Complex Structure of Receptive Fields in the Middle Temporal Area. *Frontiers in Systems Neuroscience*, 7, 2.  
<https://doi.org/10.3389/fnsys.2013.00002>
- Rosenbaum, D. A. (2010). *Human motor control* (2nd ed). Elsevier Inc.
- Rouse, A. G., Mazurek, K. A., Liu, Z., Rivlis, G., & Schieber, M. H. (2018). How Separate Are Reaching and Grasping? In *Reach-to-Grasp Behavior*. Routledge.
- RStudio Team. (2020). *RStudio: Integrated development environment for r* [Manual].  
<http://www.rstudio.com/>
- Russo, J. E. (2019). Eye Fixations as a Process Trace. In *A Handbook of Process Tracing Methods* (2nd ed.). Routledge.
- Sainburg, R. L. (2015). Should the Equilibrium Point Hypothesis (EPH) be Considered a Scientific Theory? *Motor Control*, 19(2), 142–148. <https://doi.org/10.1123/mc.2014-0056>
- Schaal, S., Mohajerian, P., & Ijspeert, A. (2007). Dynamics systems vs. Optimal control—A unifying view. In P. Cisek, T. Drew, & J. F. Kalaska (Eds.), *Progress in Brain Research* (Vol. 165, pp. 425–445). Elsevier. [https://doi.org/10.1016/S0079-6123\(06\)65027-9](https://doi.org/10.1016/S0079-6123(06)65027-9)
- Schall, J. D. (2001). Neural basis of deciding, choosing and acting. *Nature Reviews Neuroscience*, 2(1), 33–42. <https://doi.org/10.1038/35049054>
- Schneider, I. K., van Harreveld, F., Rotteveel, M., Topolinski, S., van der Pligt, J., Schwarz, N., & Koole, S. L. (2015). The path of ambivalence: Tracing the pull of opposing evaluations using mouse trajectories. *Frontiers in Psychology*, 0.  
<https://doi.org/10.3389/fpsyg.2015.00996>

Schöner, G. (2008). Dynamical systems approaches to cognition. In *The Cambridge handbook of computational psychology* (pp. 101–126). Cambridge University Press.

<https://doi.org/10.1017/CBO9780511816772.007>

Schulte-Mecklenbeck, M., Anton Kuehberger, & Joseph G. Johnson. (2019). *A Handbook of Process Tracing Methods: 2nd Edition: Vol. Second edition*. Routledge.

<https://search.ebscohost.com/login.aspx?direct=true&db=nlebk&AN=2092299&site=ehost-live>

Schulte-Mecklenbeck, M., Johnson, J. G., Böckenholt, U., Goldstein, D. G., Russo, J. E., Sullivan, N. J., & Willemsen, M. C. (2017). Process-Tracing Methods in Decision Making: On Growing Up in the 70s. *Current Directions in Psychological Science*, 26(5), 442–450.

<https://doi.org/10.1177/0963721417708229>

Shadmehr, R., & Mussa-Ivaldi, F. A. (1994). Adaptive representation of dynamics during learning of a motor task. *Journal of Neuroscience*, 14(5), 3208–3224.

<https://doi.org/10.1523/JNEUROSCI.14-05-03208.1994>

Shi, Y., & Buneo, C. A. (2012). Movement variability resulting from different noise sources: A simulation study. *Human Movement Science*, 31(4), 772–790.

<https://doi.org/10.1016/j.humov.2011.07.003>

Simon, J. R. (1990). The Effects of an Irrelevant Directional CUE on Human Information Processing. In R. W. Proctor & T. G. Reeve (Eds.), *Advances in Psychology* (Vol. 65, pp. 31–86). North-Holland. [https://doi.org/10.1016/S0166-4115\(08\)61218-2](https://doi.org/10.1016/S0166-4115(08)61218-2)

Smeding, A., Quinton, J.-C., Lauer, K., Barca, L., & Pezzulo, G. (2016). Tracking and simulating dynamics of implicit stereotypes: A situated social cognition perspective. *Journal of Personality and Social Psychology*, 111(6), 817–834.

<https://doi.org/10.1037/pspa0000063>

Song, J.-H., & Nakayama, K. (2008). Numeric comparison in a visually-guided manual reaching task. *Cognition*, 106(2), 994–1003. <https://doi.org/10.1016/j.cognition.2007.03.014>

- Song, J.-H., & Nakayama, K. (2009). Hidden cognitive states revealed in choice reaching tasks. *Trends in Cognitive Sciences*, 13(8), 360–366. <https://doi.org/10.1016/j.tics.2009.04.009>
- Spivey, M. J. (2008). *The Continuity of Mind*. Oxford University Press.
- Spivey, M. J., & Dale, R. (2004). On the continuity of mind: Toward a dynamical account of cognition. In *The psychology of learning and motivation: Advances in research and theory*, Vol 45 (pp. 87–142). Elsevier Academic Press.
- Spivey, M. J., & Dale, R. (2006). Continuous Dynamics in Real-Time Cognition. *Current Directions in Psychological Science*, 15(5), 207–211. <https://doi.org/10.1111/j.1467-8721.2006.00437.x>
- Spivey, M. J., Grosjean, M., & Knoblich, G. (2005). Continuous attraction toward phonological competitors. *Proceedings of the National Academy of Sciences*, 102(29), 10393–10398. <https://doi.org/10.1073/pnas.0503903102>
- Stanislaw, H., & Todorov, N. (1999). Calculation of signal detection theory measures. *Behavior Research Methods, Instruments, & Computers*, 31(1), 137–149. <https://doi.org/10.3758/BF03207704>
- Stasinopoulos, M., Rigby, B., Voudouris, V., Akantziliotou, C., Enea, M., & Kiose, D. (2021). *gamlss: Generalised Additive Models for Location Scale and Shape* (5.3-4) [Computer software]. <https://CRAN.R-project.org/package=gamlss>
- Stillman, P. E., Medvedev, D., & Ferguson, M. J. (2017). Resisting Temptation: Tracking How Self-Control Conflicts Are Successfully Resolved in Real Time. *Psychological Science*, 28(9), 1240–1258. <https://doi.org/10.1177/0956797617705386>
- Stillman, P. E., Shen, X., & Ferguson, M. J. (2018). How Mouse-tracking Can Advance Social Cognitive Theory. *Trends in Cognitive Sciences*, 22(6), 531–543. <https://doi.org/10.1016/j.tics.2018.03.012>
- Stone, M. (1960). Models for choice-reaction time. *Psychometrika*, 25(3), 251–260. <https://doi.org/10.1007/BF02289729>



- Sullivan, N. J., & Huettel, S. A. (2021). Healthful choices depend on the latency and rate of information accumulation. *Nature Human Behaviour*, 1–9.  
<https://doi.org/10.1038/s41562-021-01154-0>
- Suzuki, M., Yamazaki, Y., Mizuno, N., & Matsunami, K. (1997). Trajectory formation of the center-of-mass of the arm during reaching movements. *Neuroscience*, 76(2), 597–610.  
[https://doi.org/10.1016/S0306-4522\(96\)00364-8](https://doi.org/10.1016/S0306-4522(96)00364-8)
- Tanner Jr., W. P., & Swets, J. A. (1954). A decision-making theory of visual detection. *Psychological Review*, 61, 401–409. <https://doi.org/10.1037/h0058700>
- Thura, D., Beauregard-Racine, J., Fradet, C.-W., & Cisek, P. (2012). Decision making by urgency gating: Theory and experimental support. *Journal of Neurophysiology*, 108(11), 2912–2930. <https://doi.org/10.1152/jn.01071.2011>
- Thura, D., & Cisek, P. (2014). Deliberation and commitment in the premotor and primary motor cortex during dynamic decision making. *Neuron*, 81(6), 1401–1416.  
<https://doi.org/10.1016/j.neuron.2014.01.031>
- Tillman, G., Van Zandt, T., & Logan, G. D. (2020). Sequential sampling models without random between-trial variability: The racing diffusion model of speeded decision making. *Psychonomic Bulletin & Review*, 27(5), 911–936. <https://doi.org/10.3758/s13423-020-01719-6>
- Tipper, S. P., Howard, L. A., & Jackson, S. R. (1997). Selective Reaching to Grasp: Evidence for Distractor Interference Effects. *Visual Cognition*, 4(1), 1–38.  
<https://doi.org/10.1080/713756749>
- Tipper, S. P., Weaver, B., & Houghton, G. (1994). Behavioural Goals Determine Inhibitory Mechanisms of Selective Attention. *The Quarterly Journal of Experimental Psychology Section A*, 47(4), 809–840. <https://doi.org/10.1080/14640749408401098>
- Todorov, E., & Jordan, M. I. (2002). Optimal feedback control as a theory of motor coordination. *Nature Neuroscience*, 5(11), 1226–1235. <https://doi.org/10.1038/nn963>

- Tolman, E. C. (1926). A behavioristic theory of ideas. *Psychological Review*, 33(5), 352–369.  
<https://doi.org/10.1037/h0070532>
- Trenholm, S., & Krishnaswamy, A. (2020). An Annotated Journey through Modern Visual Neuroscience. *Journal of Neuroscience*, 40(1), 44–53.  
<https://doi.org/10.1523/JNEUROSCI.1061-19.2019>
- Trommershäuser, J., Gepshtein, S., Maloney, L. T., Landy, M. S., & Banks, M. S. (2005). Optimal Compensation for Changes in Task-Relevant Movement Variability. *The Journal of Neuroscience*, 25(31), 7169–7178. <https://doi.org/10.1523/JNEUROSCI.1906-05.2005>
- Ulbrich, P., & Gail, A. (2021). The cone method: Inferring decision times from single-trial 3D movement trajectories in choice behavior. *Behavior Research Methods*, 53(6), 2456–2472. <https://doi.org/10.3758/s13428-021-01579-5>
- Usher, M., & McClelland, J. L. (2001). The time course of perceptual choice: The leaky, competing accumulator model. *Psychological Review*, 108(3), 550–592.  
<https://doi.org/10.1037/0033-295x.108.3.550>
- Valyear, K. F., Culham, J. C., Sharif, N., Westwood, D., & Goodale, M. A. (2006). A double dissociation between sensitivity to changes in object identity and object orientation in the ventral and dorsal visual streams: A human fMRI study. *Neuropsychologia*, 44(2), 218–228. <https://doi.org/10.1016/j.neuropsychologia.2005.05.004>
- van Beers, R. J., Haggard, P., & Wolpert, D. M. (2004). The Role of Execution Noise in Movement Variability. *Journal of Neurophysiology*, 91(2), 1050–1063.  
<https://doi.org/10.1152/jn.00652.2003>
- van den Berg, R., Anandalingam, K., Zylberberg, A., Kiani, R., Shadlen, M. N., & Wolpert, D. M. (2016). A common mechanism underlies changes of mind about decisions and confidence. *ELife*, 5, e12192. <https://doi.org/10.7554/eLife.12192>

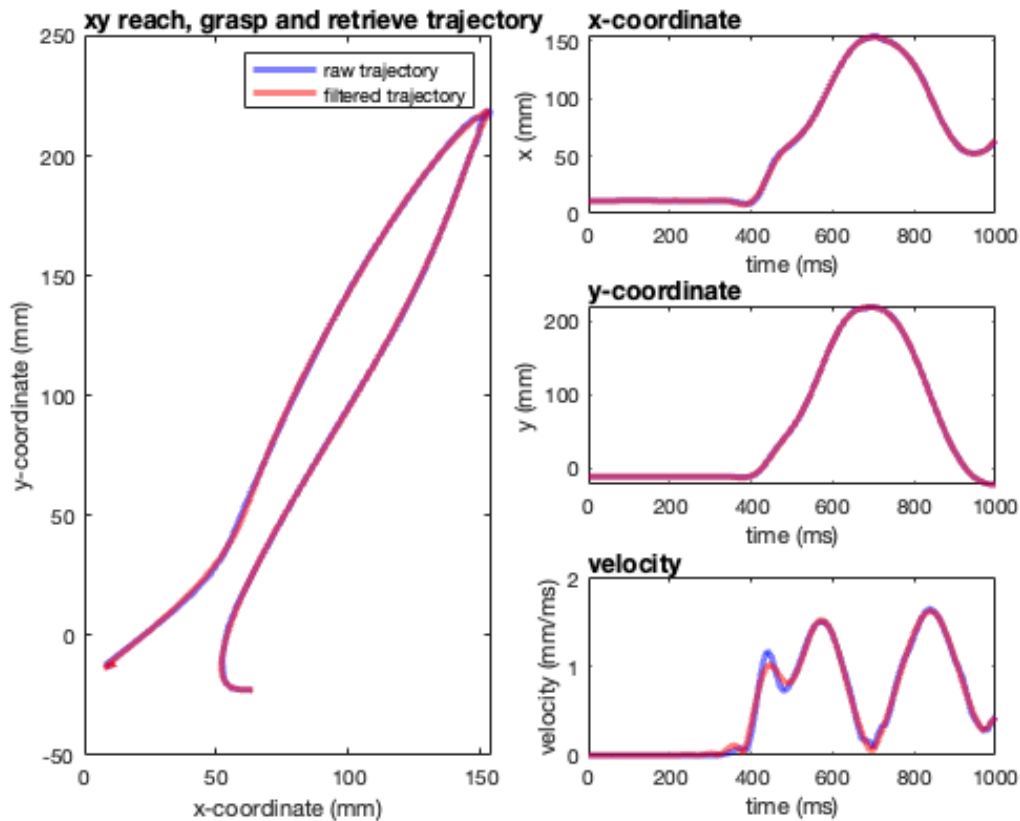
- Van der Stigchel, S., Meeter, M., & Theeuwes, J. (2006). Eye movement trajectories and what they tell us. *Neuroscience & Biobehavioral Reviews*, 30(5), 666–679.  
<https://doi.org/10.1016/j.neubiorev.2005.12.001>
- van Polanen, V., & Davare, M. (2015). Interactions between dorsal and ventral streams for controlling skilled grasp. *Neuropsychologia*, 79, 186–191.  
<https://doi.org/10.1016/j.neuropsychologia.2015.07.010>
- Vandenbergh, A., Levin, O., De Schutter, J., Swinnen, S., & Jonkers, I. (2010). Three-dimensional reaching tasks: Effect of reaching height and width on upper limb kinematics and muscle activity. *Gait & Posture*, 32(4), 500–507. <https://doi.org/10.1016/j.gaitpost.2010.07.009>
- Verheij, R., Brenner, E., & Smeets, J. B. J. (2012). Grasping Kinematics from the Perspective of the Individual Digits: A Modelling Study. *PLOS ONE*, 7(3), e33150.  
<https://doi.org/10.1371/journal.pone.0033150>
- Verheij, R., Brenner, E., & Smeets, J. B. J. (2013). Why are the digits' paths curved vertically in human grasping movements? *Experimental Brain Research*, 224(1), 59–68.  
<https://doi.org/10.1007/s00221-012-3288-0>
- Voudouris, D., Smeets, J. B. J., & Brenner, E. (2013). Ultra-fast selection of grasping points. *Journal of Neurophysiology*, 110(7), 1484–1489. <https://doi.org/10.1152/jn.00066.2013>
- Wagenmakers, E.-J., & Farrell, S. (2004). AIC model selection using Akaike weights. *Psychonomic Bulletin & Review*, 11(1), 192–196. <https://doi.org/10.3758/BF03206482>
- Wald, A., & Wolfowitz, J. (1948). Optimum Character of the Sequential Probability Ratio Test. *The Annals of Mathematical Statistics*, 19(3), 326–339.  
<https://doi.org/10.1214/aoms/1177730197>
- Welsh, T. N., & Elliott, D. (2004). Movement Trajectories in the Presence of a Distracting Stimulus: Evidence for a Response Activation Model of Selective Reaching. *The Quarterly Journal of Experimental Psychology Section A*, 57(6), 1031–1057.  
<https://doi.org/10.1080/02724980343000666>

- Welsh, T. N., Elliott, D., & Weeks, D. J. (1999). Hand deviations toward distractors: Evidence for response competition. *Experimental Brain Research*, 127(2), 207–212.  
<https://doi.org/10.1007/s002210050790>
- Wisniewski, N. J., Gallivan, J. P., & Chapman, C. S. (2020). Models, movements, and minds: Bridging the gap between decision making and action. *Annals of the New York Academy of Sciences*, 1464(1), 30–51. <https://doi.org/10.1111/nyas.13973>
- Wong JD, Cluff T, Kuo AD. (2020). The energetic basis for smooth human arm movements. *Elife*. 2021 Dec 20;10:e68013. doi: 10.7554/eLife.68013. PMID: 34927584; PMCID: PMC8741215.
- Wong, A. L., & Haith, A. M. (2017). Motor planning flexibly optimizes performance under uncertainty about task goals. *Nature Communications*, 8(1), 14624.  
<https://doi.org/10.1038/ncomms14624>
- Wong, A. L., Haith, A. M., & Krakauer, J. W. (2015). Motor Planning. *The Neuroscientist*, 21(4), 385–398. <https://doi.org/10.1177/1073858414541484>
- Woodworth, R. S. (1899). Accuracy of voluntary movement. *The Psychological Review: Monograph Supplements*, 3(3), i–114. <https://doi.org/10.1037/h0092992>
- Yellott, J. I. (1971). Correction for fast guessing and the speed-accuracy tradeoff in choice reaction time. *Journal of Mathematical Psychology*, 8(2), 159–199.  
[https://doi.org/10.1016/0022-2496\(71\)90011-3](https://doi.org/10.1016/0022-2496(71)90011-3)
- Yeo, S.-H., Franklin, D. W., & Wolpert, D. M. (2016). When Optimal Feedback Control Is Not Enough: Feedforward Strategies Are Required for Optimal Control with Active Sensing. *PLOS Computational Biology*, 12(12), e1005190.  
<https://doi.org/10.1371/journal.pcbi.1005190>
- Yoo, S. B. M., Hayden, B. Y., & Pearson, J. M. (2021). Continuous decisions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 376(1819), 20190664.  
<https://doi.org/10.1098/rstb.2019.0664>



Appendix A: Additional Figures for Chapter 2

Figure 0-1 Raw and filtered position and derivative of a single trial from experiment 1



The figure shows the raw trajectory in blue, and the trajectory after filtering with a low-pass filter with a cut-off frequency at 10Hz. These lines are overlaid at most points in the trajectory on the left hand panel, as well as the coordinate by time plots on the right side.

The following tables detail a range of alternative analyses of the dependent variables reported in Chapter 2.

The table rows are the factors which tended to survive after backwards stepwise selection based on how they improved the AIC of each model. The table columns represent an alternative analysis approach, i.e., different transforms applied to the dependent variable of interest, whether analysis was split between left and right reaches, and whether the analysis was conducted on all reach actions which were correct, or only on reached which were not categorised as changes of mind.

Table 0-1 Effects vs analysis – Experiment 1 Initiation Time

	Analysis of all correct reach trials					Analysis without change of mind trials				
Effect:	S1: 1/IT	S1: raw IT	S1: log(IT)	S1: 1/IT (left)	S1: 1/IT (right)	S1: 1/IT	S1: raw IT	S1: log(IT)	S1: 1/IT (left)	S1: 1/IT (right)
Difficulty	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>
Target Side	Yes	No	No	NA	NA	No	No	No	NA	NA
Target Orientation	Yes	No	No	No	Yes	No	No	No	No	Yes
Orientation x Side	Yes	No	Yes	NA	NA	No	No	No	NA	No
Difficulty x Side	No	Yes	Yes	NA	NA	Yes	Yes	Yes	NA	No
Difficulty x Orientation	No	No	No	No	No	No	No	No	No	No
Distractor Congruency	No	No	No	No	No	No	No	No	No	No

Note. Alternative approaches to the analysis of initiation time included the reciprocal, the raw time, the logarithm of time, and splitting the reciprocal

transformation into left and right reaches. No analysis choice removed the effect of Difficulty from initiation time, however workspace effects were present in some of the analyses, but not others.

A repeated measures ANOVA analysis was used to compare median initiation times across between the effects of choice difficulty, target side, target orientation, and distractor congruency, and all interactions of these factors (using the `aov_4` function from the `afex` package (Singmann et al., 2023)). Only the effect of choice difficulty was statistically significant ( $F(1,31)=24.04$ ,  $p<0.001$ ) with no other differences reaching statistical significance. This analysis was repeated with change of mind trials removed, and here again there was an influence of choice difficulty ( $F(1,31)=35.60$ ,  $p<0.001$ ), while no other factors reached statistical significance.



Table 0-2 Effects vs Analysis choice – Experiment 1 Movement Time

	Analysis of all correct reach trials					Analysis without change of mind trials				
Effect:	S1: 1/MT	S1: raw MT	S1: mean velocity	S1: peak Velocity		S1: 1/MT	S1: raw MT	S1: mean velocity	S1: peak velocity	
Difficulty	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>		<b>Yes</b>	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>	
Target Side	Yes	Yes	Yes	Yes		Yes	Yes	Yes	Yes	
Target Orientation	No	Yes	Yes	Yes		No	No	Yes	Yes	
Orientation x Side	Yes	Yes	Yes	Yes		Yes	Yes	No	Yes	
Difficulty x Side	No	No	No	No		No	No	No	No	
Difficulty x Orientation	No	No	No	No		No	No	No	No	
Distractor Congruency	Yes	Yes	Yes	No		Yes	No	No	No	

Note. For analyses of movement time in study 1, difficulty was present in all analyses, as was the influence of target side. The influence of target orientation, i.e. whether the target was horizontal or vertical, was sensitive to how movement time was used in the analysis, as was whether the distractor was oriented the same as the target.

A repeated measures ANOVA analysis was also conducted on the median movement times for study 1. There was a significant main effect of choice difficulty ( $F(1,31)=24.34$ ,  $p<0.001$ ), target side ( $F(1,31)=62.83$ ,  $p<0.001$ ), target orientation ( $F(1,31)=5.49$ ,  $p=0.026$ ) and the interaction between target side and orientation ( $F(1,31)=90.10$ ,  $p<0.001$ ). This pattern was mostly repeated for the ANOVA analysis with changes of mind removed, with choice difficulty ( $F(1,31)=16.66$ ,  $p<0.001$ ), target side ( $F(1,31)=65.29$ ,  $p<0.001$ ), and the interaction between target side and target orientation ( $F(1,31)=57.91$ ,  $p<0.001$ ), but the main effect of target orientation was no longer significant at the  $p<0.05$  level ( $F(1,31)=3.33$ ,  $p=0.078$ ).

Table 0-3 Effect vs Analysis choice – Experiment 1 Overall Time

	Analysis of all correct reach trials					Analysis without change of mind trials				
Effect:	S1: 1/OT	S1: raw OT	S1: log OT			S1: 1/MT	S1: raw MT	S1: mean velocity		
Difficulty	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>			<b>Yes</b>	<b>Yes</b>	<b>Yes</b>		
Target Side	Yes	Yes	Yes			Yes	Yes	Yes		
Target Orientation	No	No	No			No	No	No		
Orientation x Side	Yes	Yes	Yes			Yes	Yes	Yes		
Difficulty x Side	No	No	No			Yes	Yes	Yes		
Difficulty x Orientation	No	No	No			No	No	No		
Distractor Congruency	No	No	No			No	No	No		

Analyses of overall time could be entered as the reciprocal, or as the raw time, or as the logarithm of time. The notable change across these analyses was that removing “change of mind” trials led to an interaction between overall speed and choice difficulty.

A repeated measures ANOVA was conducted on the median overall time for study 1, with choice difficulty ( $F(1,31)=65.11$ ,  $p<0.001$ ), target side ( $F(1,31)=43.11$ ,  $p<0.001$ ) and the target side and target orientation interaction ( $F(1,31)=43.36$ ,  $p<0.001$ ) reaching significance. Removing the change of mind trials from the analysis retained the same pattern of results with significant main effects of choice difficulty ( $F(1,31)=42.13$ ,  $p<0.001$ ) and target side ( $F(1,31)=28.62$ ,  $p<0.001$ ) and the interaction of target side and orientation being significant at the  $p<0.05$  level ( $F(1,31)=28.94$ ,  $p<0.001$ ).

Table 0-4 Effect vs Analysis choice – Experiment 1 Curvature

	Analysis of all correct reach trials			Analysis without change of mind trials		
Effect:	S1: AUC	S1: AUC (left)	S1: AUC (right)	S1: AUC	S1: AUC (left)	S1: AUC (right)
Difficulty	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>	<b>No</b>	<b>No</b>	<b>Yes</b>
Target Side	Yes	NA	NA	Yes	NA	NA
Target Orientation	Yes	Yes	Yes	Yes	Yes	Yes
Orientation x Side	Yes	NA	NA	Yes	NA	NA
Difficulty x Side	No	No	No	<b>Yes</b>	NA	NA
Difficulty x Orientation	No	No	No	No	Yes	No
Distractor Congruency	No	No	No	No	No	No
Orientation x Congruency	No	No	Yes	No	No	Yes

Note. Path curvature, as measured by AUC, could be decomposed into leftward and rightwards reaches. When change of mind trials were removed from these data and the data sets were split by target side, there was still an influence of choice difficulty on reaches to right hand side targets.

A repeated measures ANOVA on median AUC values revealed statistically significant main effects of choice difficulty ( $F(1,31)=20.79$ ,  $p<0.001$ ), target side ( $F(1,31)=48.64$ ,  $p<0.001$ ), target orientation ( $F(1,31)=21.17$ ,  $p<0.001$ ) and the interaction of target side and orientation ( $F(1,31)=16.27$ ,  $p<0.001$ ). Repeating this analysis with changes of mind retains the effect of choice difficulty ( $F(1,31)=5.28$ ,  $p=0.028$ ), target side ( $F(1,31)=51.52$ ,  $p<0.001$ ), target orientation ( $F(1,31)=25.24$ ,  $p<0.001$ ) and the interaction between target orientation and target side ( $F(1,31)=15.34$ ,  $p<0.001$ ). In this analysis there is no statistically significant effect of the interaction between choice difficulty and target side ( $F(1,31)=0.09$ ,  $p=0.772$ ), in contrast to the LMM analysis above.

Given the consistency of effects between the LMM analyses and the ANOVA, only alternative LMMs are included in the following tables.

Table 0-5 Effects vs analysis – Experiment 2 Initiation Time

	Analysis of all correct reach trials					Analysis without change of mind trials						
Effect:	S2: 1/IT	S2: raw IT	S2: log(IT)	S2: 1/IT (left)	S2: 1/IT (right)	S2: 1/IT	S2: raw IT	S2: log(IT)	S2: 1/IT (left)	S2: 1/IT (right)	S2: raw IT (left)	S2: raw IT (right)
Difficulty	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>	<b>No</b>	<b>Yes</b>	<b>Yes</b>
Target Side	No	No	No	No	No	Yes	Yes	No	NA	NA	NA	NA
Target Orientation	No	No	No	No	No	Yes	Yes	No	No	No	No	No
Orientation x Side	No	No	No	No	No	No	No	No	NA	NA	NA	NA
Difficulty x Side	No	No	No	No	No	Yes	Yes	Yes	NA	NA	NA	NA
Difficulty x Orientation	No	No	No	No	No	No	No	No	No	No	No	No
Distractor Congruency	No	No	No	No	No	Yes	Yes	No	No	Yes	No	No

Note. Alternative approaches to the analysis of initiation time included the reciprocal, the raw time, the logarithm of time, and splitting the reciprocal transformation into left and right reaches. No analysis choice removed the effect of difficulty from initiation time, aside from when reaches to the right were isolated.

Table 0-6 Effects vs Analysis choice – Experiment 2 Movement Time

	Analysis of all correct reach trials					Analysis without change of mind trials				
Effect:	S2: 1/MT	S2: raw MT	S2: mean velocity	S2: peak Velocity		S2: 1/MT	S2: raw MT	S2: mean velocity	S2: peak Velocity	
Difficulty	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>		<b>Yes</b>	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>	
Target Side	Yes	Yes	Yes	Yes		Yes	Yes	Yes	Yes	
Target Orientation	Yes	Yes	Yes	Yes		No	No	Yes	Yes	
Orientation x Side	Yes	Yes	Yes	Yes		Yes	Yes	Yes	Yes	
Difficulty x Side	No	No	No	No		No	No	No	No	
Difficulty x Orientation	No	No	No	No		No	No	No	No	
Distractor Congruency	Yes	Yes	Yes	No		Yes	No	No	No	

Note. Difficulty was always a factor on movement time whatever analyses were conducted, workspace effects are less consistent.



Table 0-7 Effect vs Analysis choice – Experiment 2 Overall Time

	Analysis of all correct reach trials			Analysis without change of mind trials		
Effect:	S2: 1/OT	S2: raw OT	S2: log OT	S2: 1/OT	S2: raw OT	S2: log OT
Difficulty	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>
Target Side	Yes	Yes	Yes	Yes	Yes	Yes
Target Orientation	No	No	No	No	No	No
Orientation x Side	Yes	Yes	Yes	Yes	Yes	Yes
Difficulty x Side	No	No	No	Yes	Yes	Yes
Difficulty x Orientation	No	No	No	No	No	No
Distractor Congruency	No	No	No	No	No	No

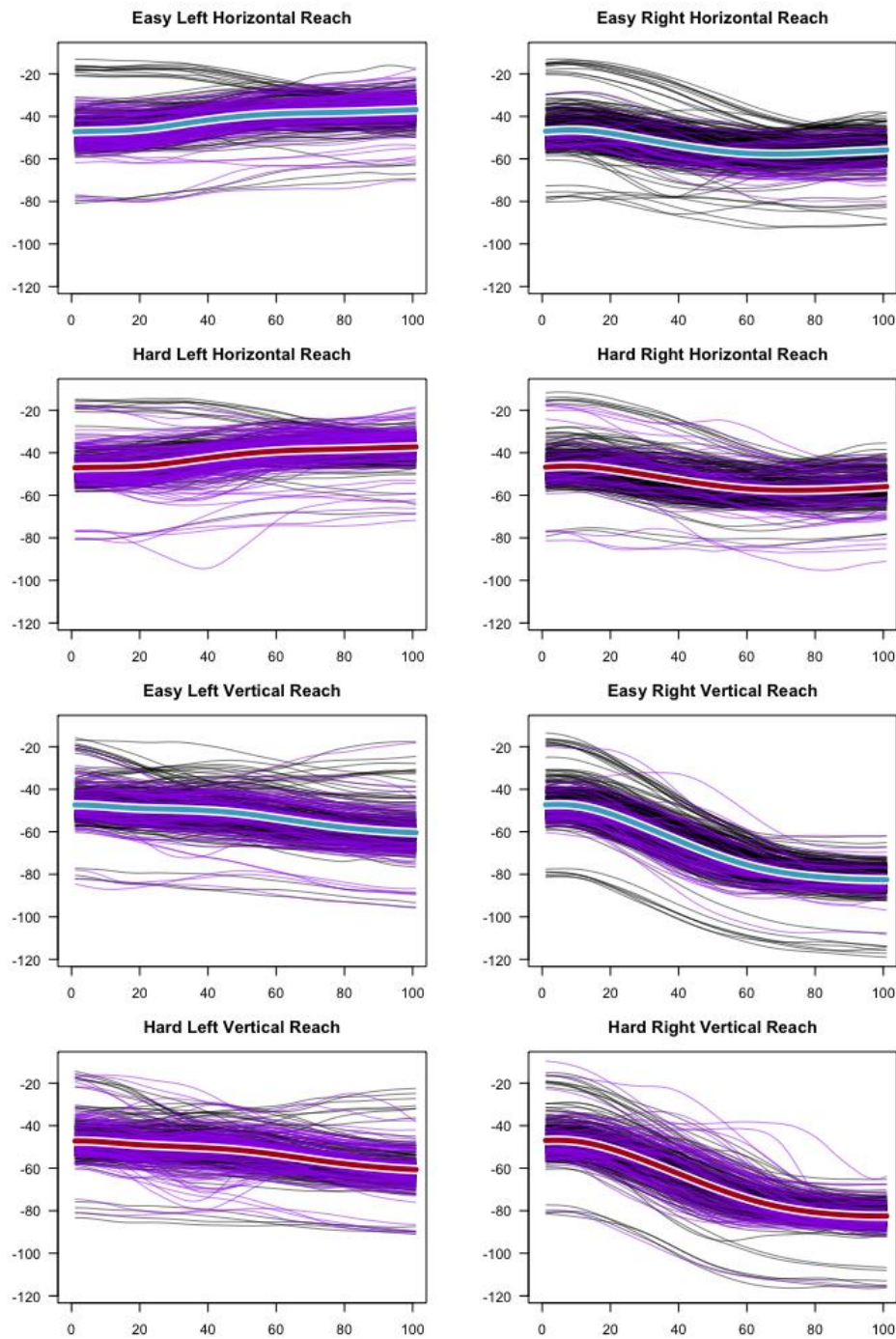
Alternative transformation of the dependent variable of overall reach time in experiment 2 did not change the pattern of results.

Table 0-8 Effect vs Analysis choice – Experiment 2 Curvature

	Analysis of all correct reach trials			Analysis without change of mind trials		
Effect:	S2: AUC	S2: AUC (left)	S2: AUC (right)	S2: AUC	S2: AUC (left)	S2: AUC (right)
Difficulty	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>	<b>No</b>	<b>Yes</b>
Target Side	Yes	NA	NA	Yes	NA	NA
Target Orientation	No	Yes	Yes	Yes	Yes	Yes
Orientation x Side	Yes	NA	NA	Yes	NA	NA
Difficulty x Side	No	NA	NA	Yes	NA	NA
Difficulty x Orientation	No	No	No	No	Yes	No
Distractor Congruency	No	No	No	No	No	No
Orientation x Congruency	No	No	No	No	No	No

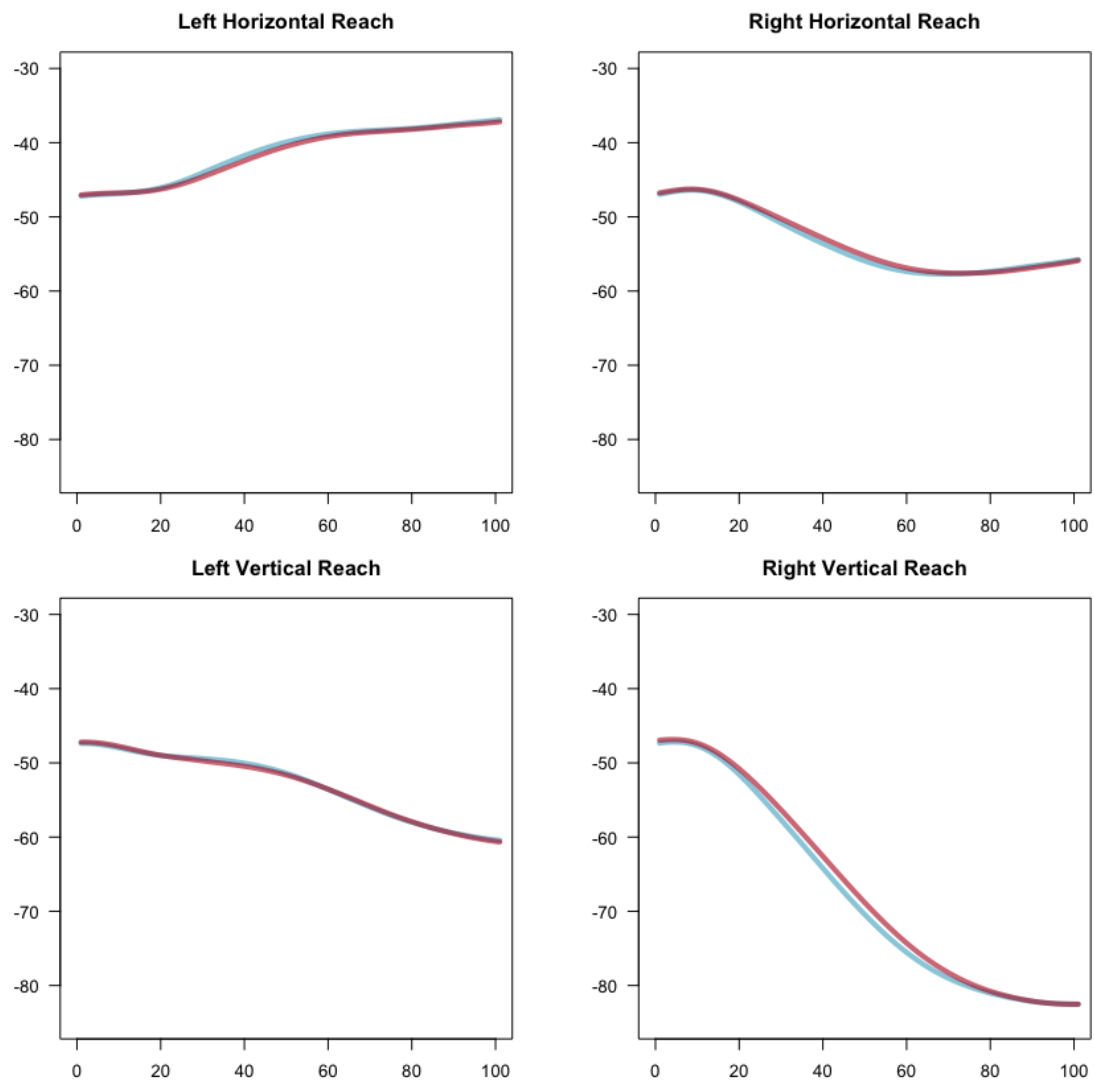
Note. The effect of difficulty was consistently present for the analyses which included all valid trials. When trials were split between left and right, the simple effect of difficulty was no longer effective for reaches to the left, but was still present in the interaction between target side and difficulty.

Figure 0-2 Wrist orientation over time in experiment 1



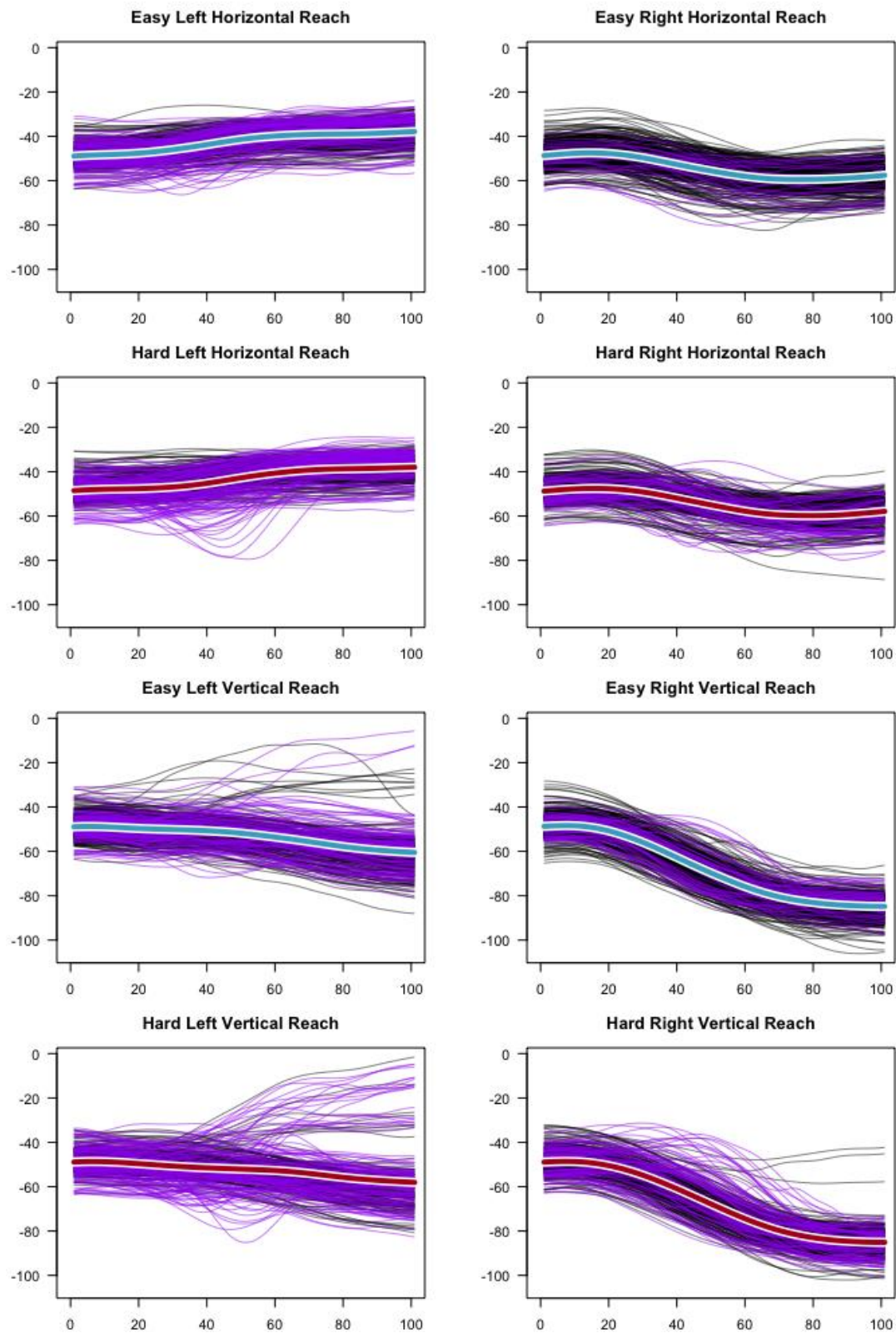
Note. Plots show the evolution of wrist orientation for all trials in study 1, with "change of mind" trials in purple, and the mean wrist orientation in either blue or red, for easy and hard trials respectively. The y-axis in these plots represents the angle against the midline made by the line between the IR markers on the knuckle and ulnar styloid of the wrist, and the x-axis represents the reach time, normalised to be between 0 and 100.

Figure 0-3 Study 1 wrist orientation traces, overlaid



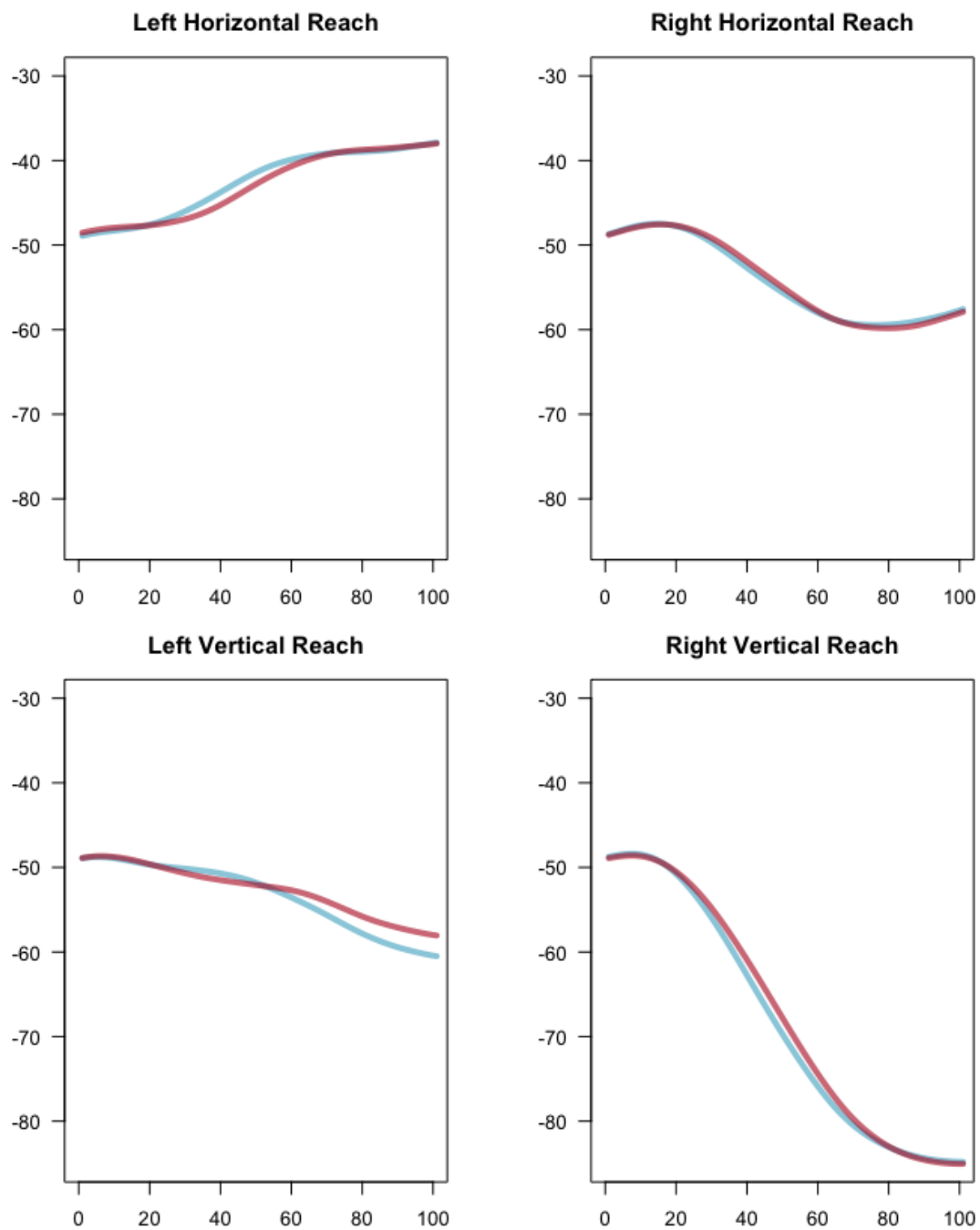
Note. Figure shows the mean wrist orientations from the previous figure with the choice difficulty overlaid. The blue lines are the easy choice reaches, and the red lines are the difficult choice reaches. The figure is divided into reaches towards targets on the left and right, and horizontal and vertical reaches.

Figure 0-4 Study 2 wrist orientation



Note. Plots show the evolution of wrist orientation for all trials in study 1, with “change of mind” trials in purple, and the mean wrist orientation in either blue or red, for easy and hard trials respectively. The y-axis in these plots represents the angle against the midline made by the line between the IR markers on the knuckle and ulnar styloid of the wrist, and the x-axis represents the reach time, normalised to be between 0 and 100.

Figure 0-5 Study 2 wrist orientation overlaid



Note. Figure shows the mean wrist orientations from the previous figure with the choice difficulty overlaid. The blue lines are the easy choice reaches, and the red lines are the difficult choice reaches. The figure is divided into reaches towards targets on the left and right, and horizontal and vertical reaches.

## Appendix B: Additional Figures for Chapter 3

Figure 0-1 Trial paths and mean path for participant 1

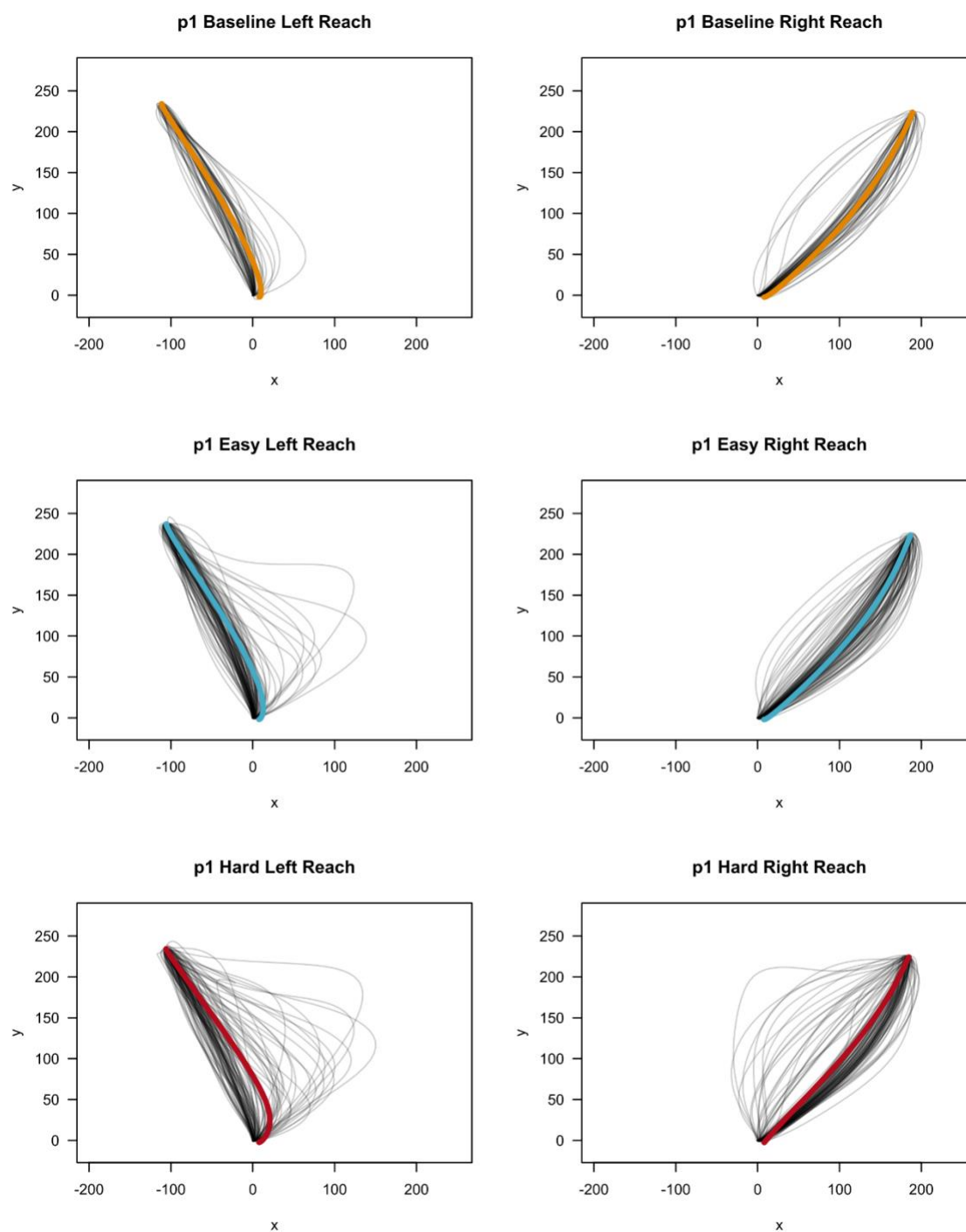


Figure 0-2 Trial paths and mean path for participant 2

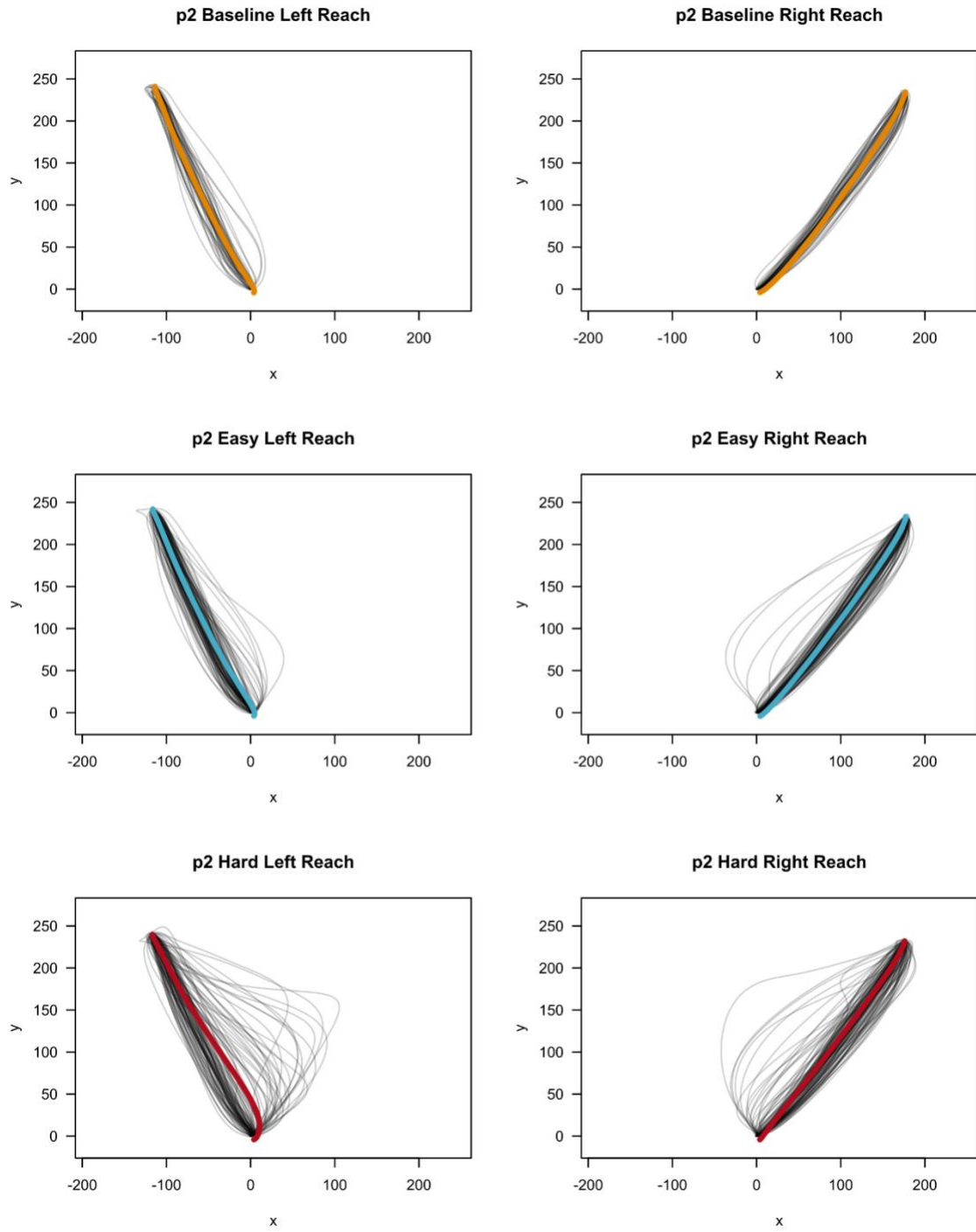


Figure 0-3 Trial paths and mean path for participant 3



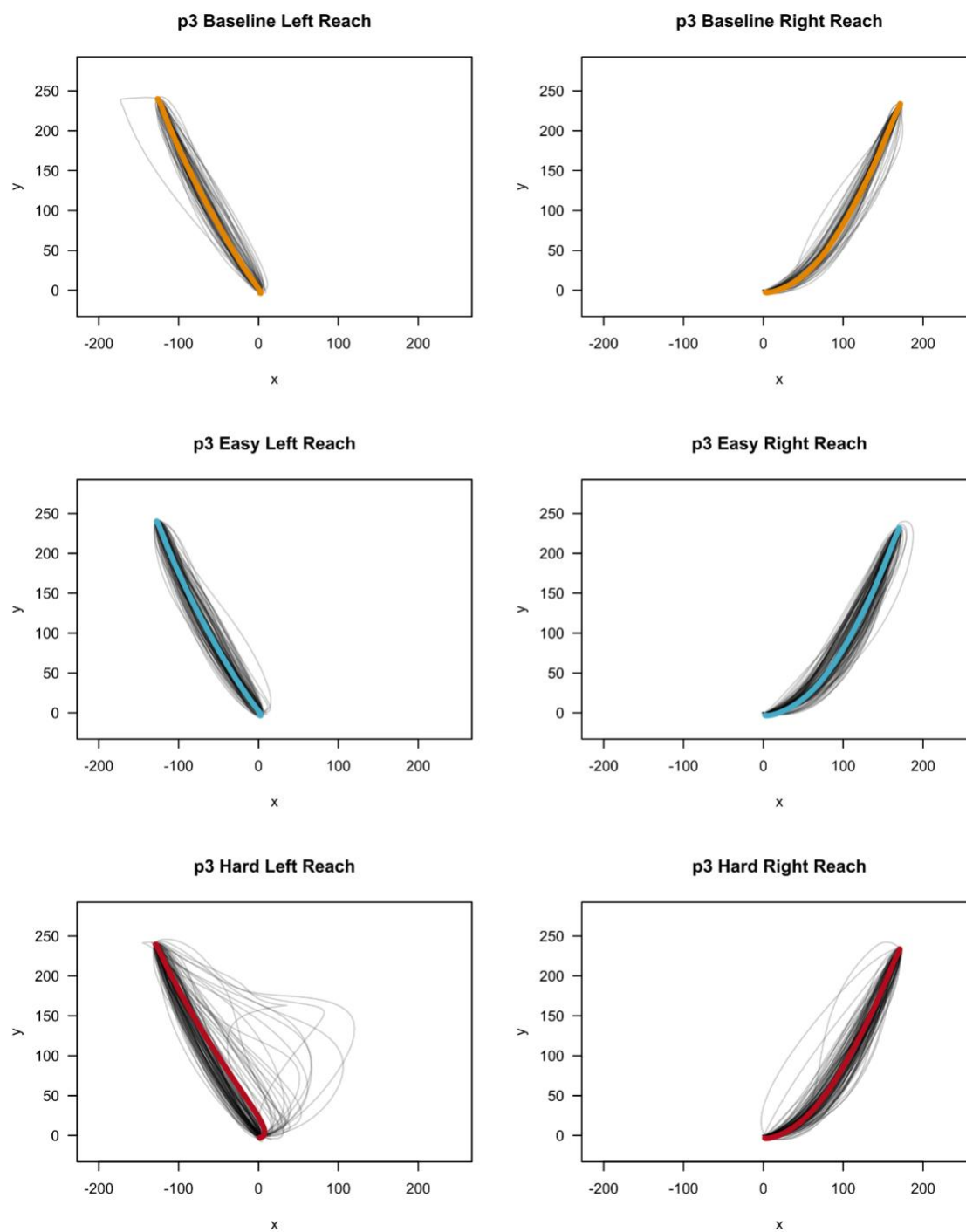


Figure 0-4 Trial paths and mean path for participant 4

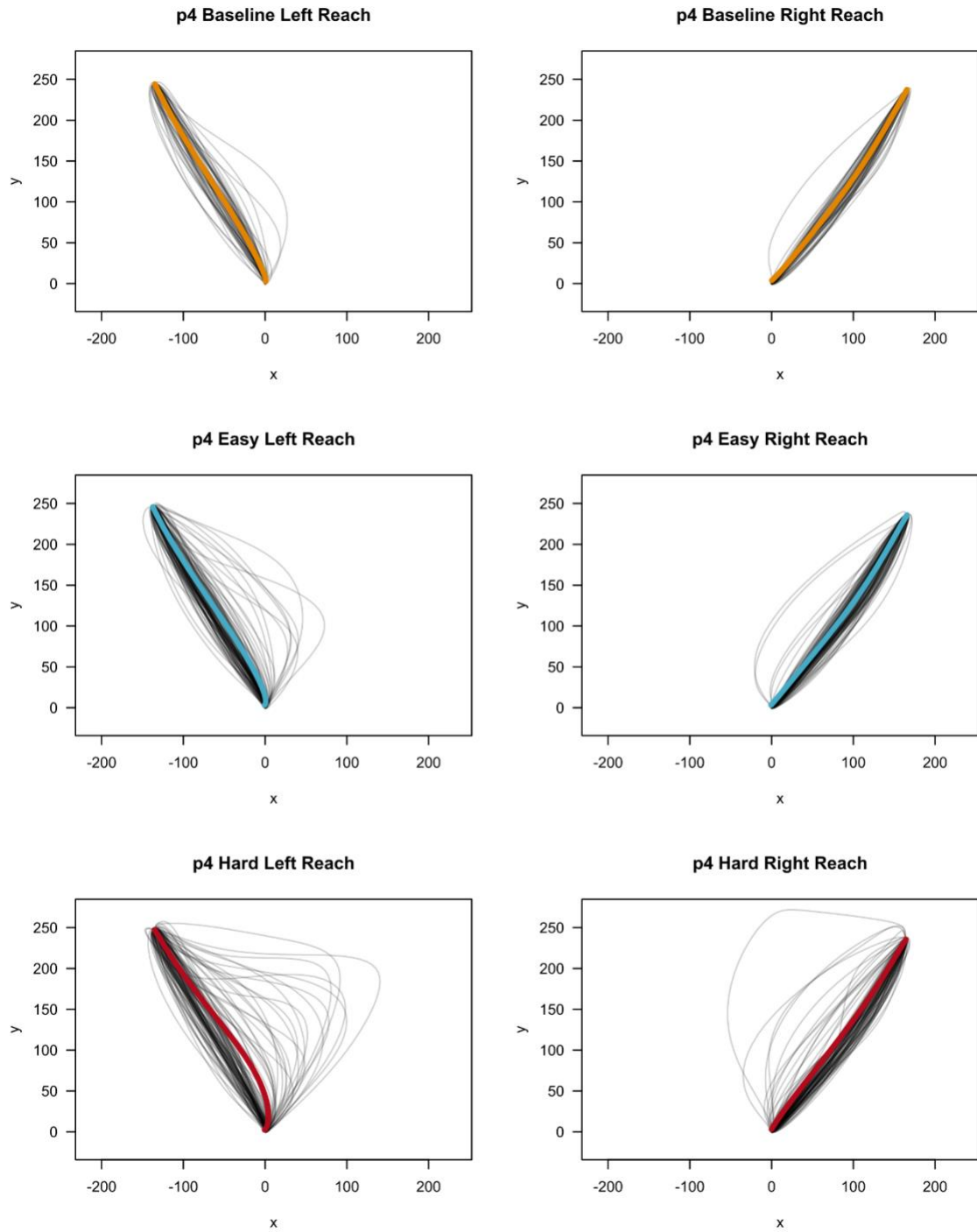


Figure 0-5 Trial paths and mean path for participant 5

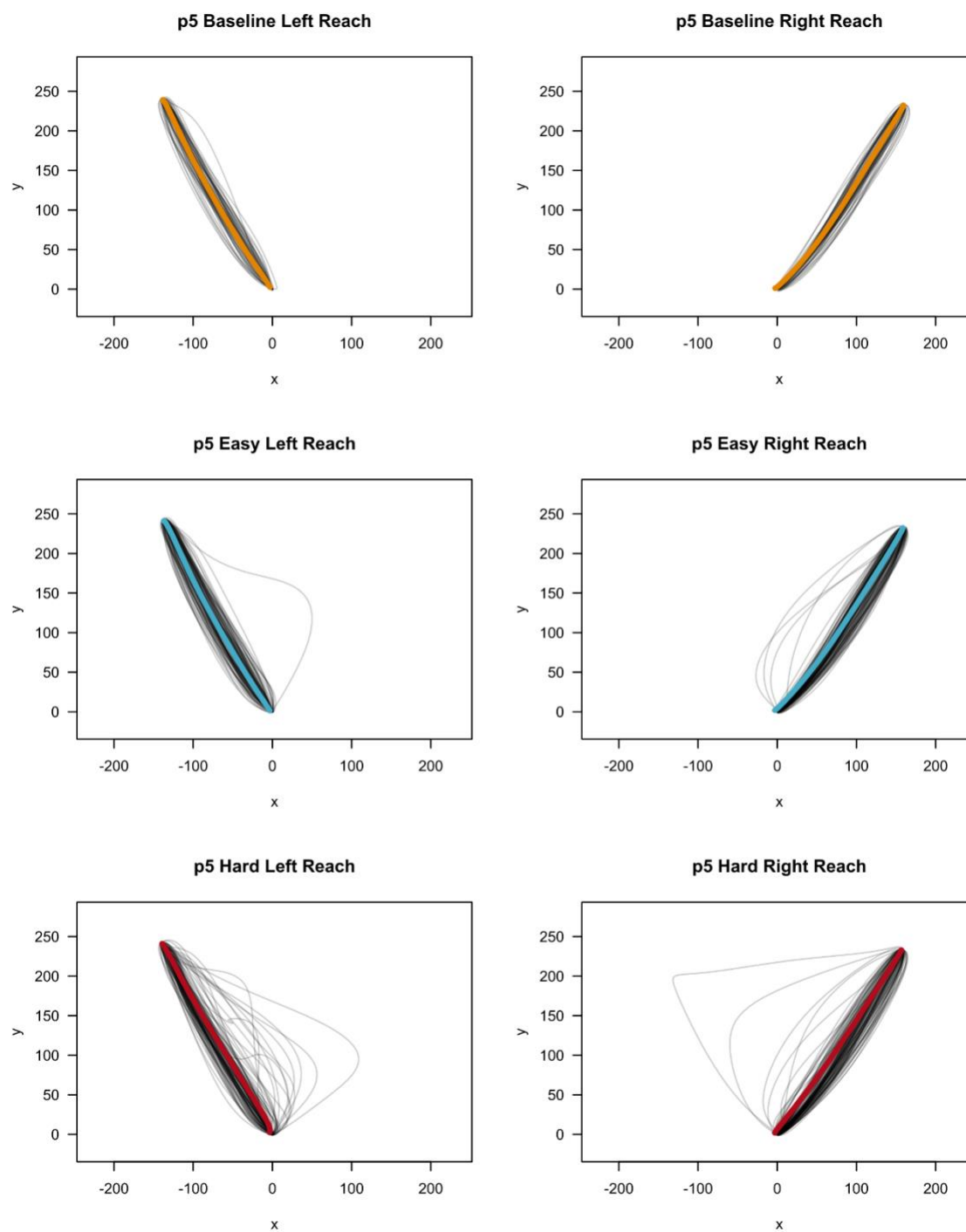


Figure 0-6 Curvature boxplot for participant 1

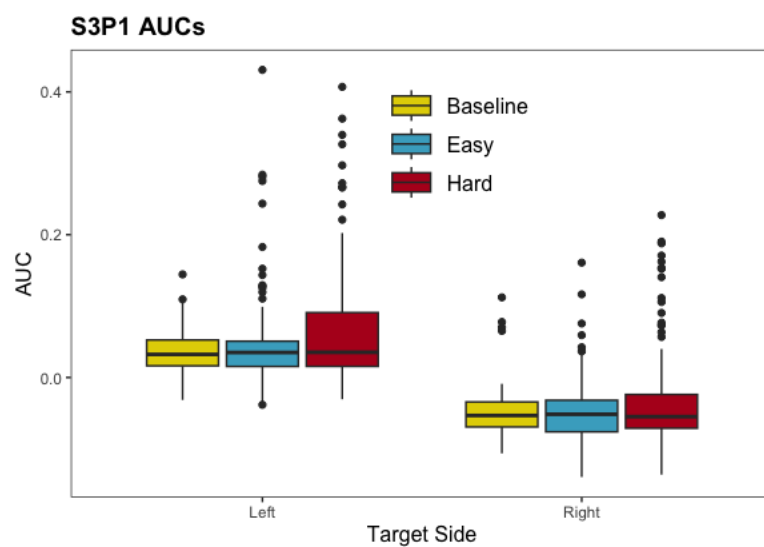


Figure 0-7 Curvature boxplot for participant 2

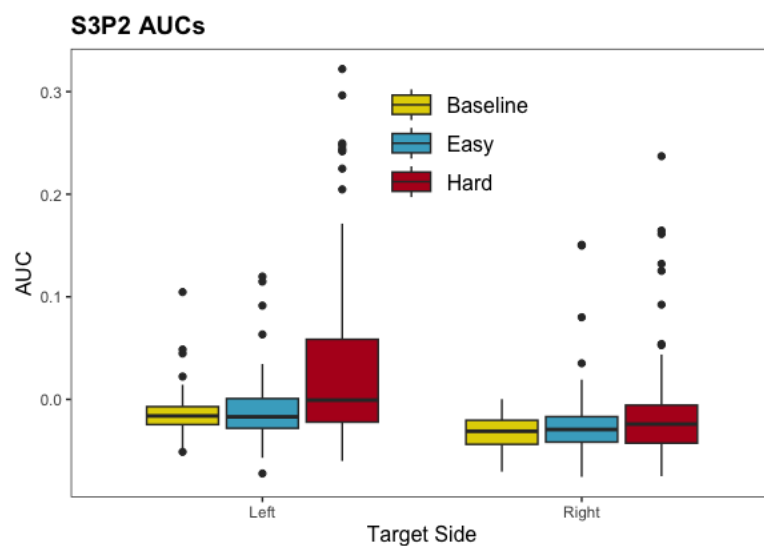


Figure 0-8 Curvature boxplot for participant 3

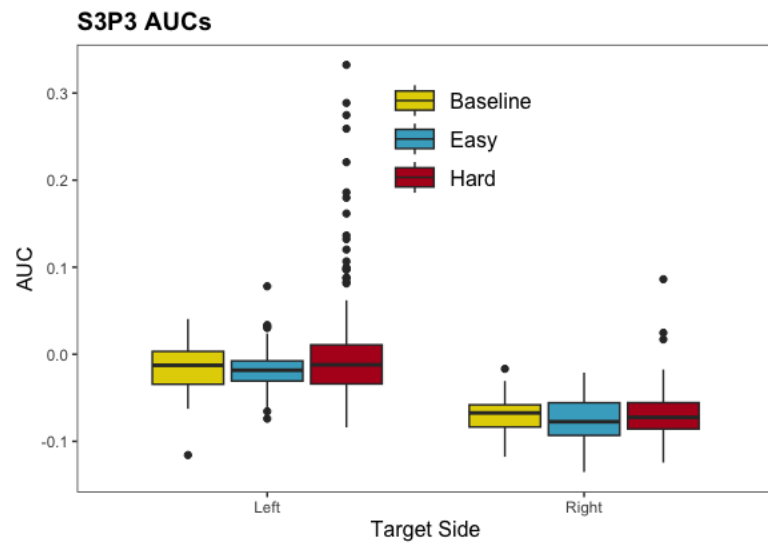


Figure 0-9 Curvature boxplot for participant 4

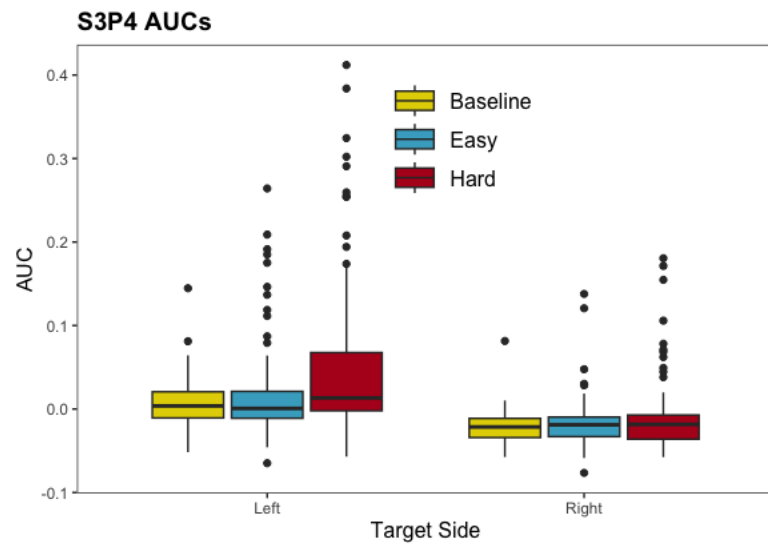


Figure 0-10 Curvature boxplot for participant 5

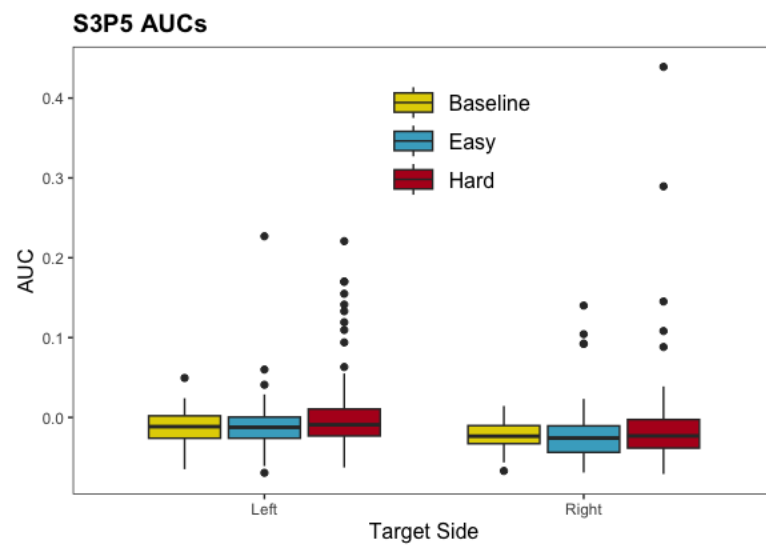
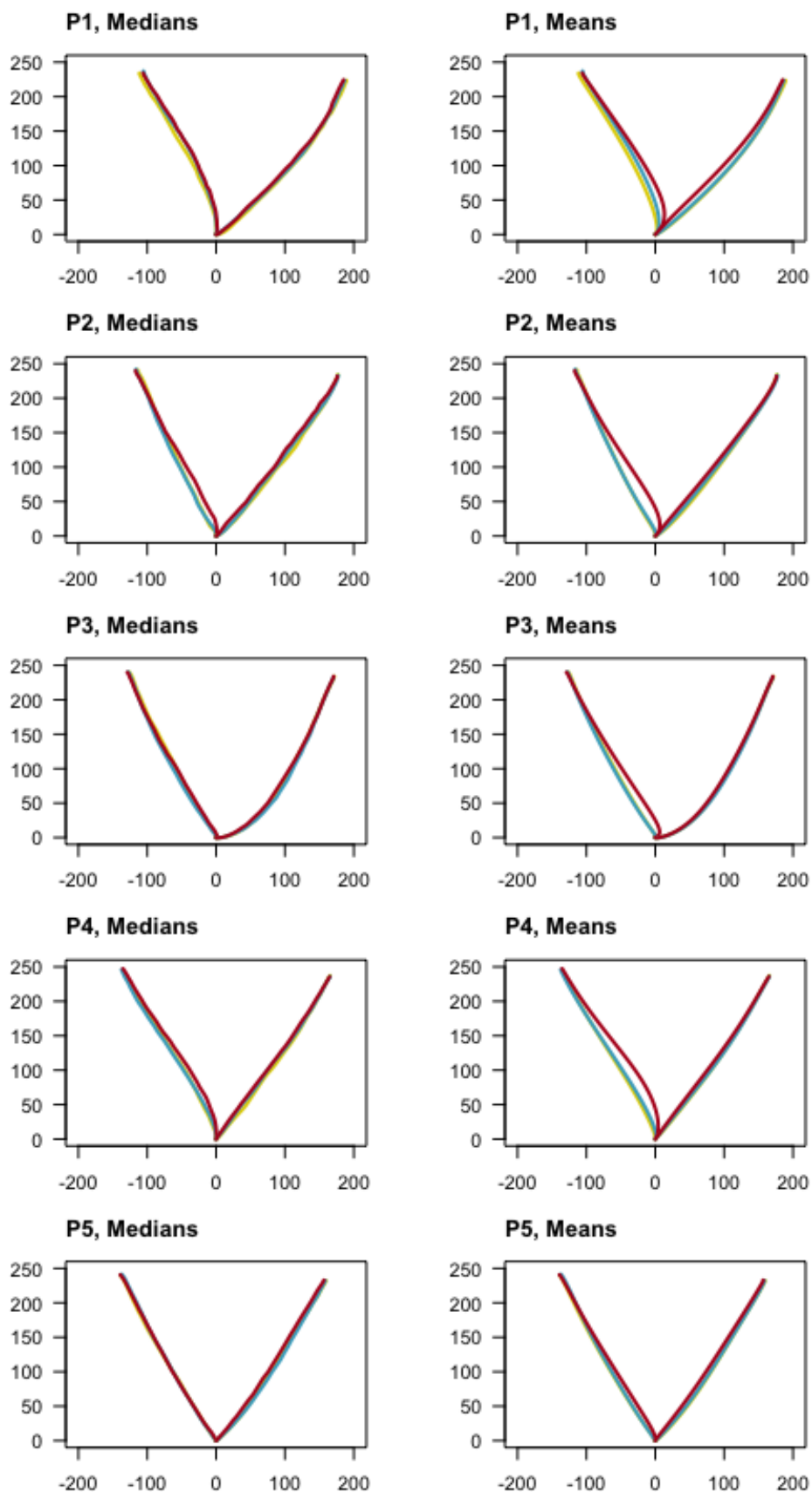


Figure 0-11 Median and mean trial paths for experiment 3



Note. Plots in the left column are the participant's median paths, while plots on in the right column are mean paths.

Linear mixed model results using all three difficulty conditions:

Function call to lmer with [measure] replaced with -1/OT, -1/IT, -1/MT or AUC, as appropriate.

The reference category for trial Difficulty was Easy trials.

```
lmer([measure] ~ (1|Participant) + Difficulty * Target_Side *  
Target_Orientation), REML = FALSE)
```

Table 0-1 Linear mixed model output comparing all difficulty conditions for experiment 3

	Overall time (inverse)	Initiation time (inverse)	Movement time (inverse)	AUC (untransformed)
(Intercept)	-1.520 (0.061) ***	-3.45 (0.19) ***	-2.99 (0.15) ***	-0.0167 (0.0075) *
Easy vs Baseline	0.0073 (0.0068)	0.027 (0.024)	-0.0042 (0.0184)	-0.0023 (0.0026)
Easy vs Hard	0.0445 (0.0056) ***	0.042 (0.020) *	0.105 (0.015) ***	0.0196 (0.0021) ***
Target Side	-0.0514 (0.0039) ***	-0.047 (0.014) ***	-0.131 (0.011) ***	-0.0214 (0.0015) ***
Target Orientation	-0.0033 (0.0039)	0.012 (0.014)	-0.014 (0.011)	0.0026 (0.0015) +
Easy vs Baseline x Target Side	-0.0030 (0.0068)	-0.025 (0.024)	0.006 (0.018)	0.0017 (0.0026)
Easy vs Hard x Target Side	-0.0024 (0.0056)	0.039 (0.020) +	-0.030 (0.015) +	-0.0082 (0.0021) ***
Easy vs Baseline x Target Orientation	0.0064 (0.0068)	0.016 (0.024)	0.011 (0.018)	0.0014 (0.0026)
Easy vs Hard x Target Orientation	0.0052 (0.0056)	-0.0083 (0.0201)	0.020 (0.015)	0.0022 (0.0021)
Target Side x Target Orientation	0.0330 (0.0039) ***	0.030 (0.014) *	0.097 (0.011) ***	0.0072 (0.0015) ***
Easy vs Baseline x Target Side x Target Orientation	-0.00034 (0.00678)	0.0093 (0.0243)	-0.0022 (0.0184)	-0.0026 (0.0026)
Easy vs Hard x Target Side x Target Orientation	-0.0047 (0.0056)	-0.023 (0.020)	0.0027 (0.0153)	0.0027 (0.0021)
SD (Intercept Participant)	0.14	0.43	0.35	0.016
SD (Observations)	0.13	0.48	0.37	0.051
Num.Obs.	2897	2897	2897	2897
R2 Marg.	0.103	0.008	0.114	0.212
R2 Cond.	0.553	0.449	0.531	0.285
AIC	-3229.9	4138	2539.2	-8792.7
BIC	-3146.3	4221.6	2622.8	-8709.1
ICC	0.5	0.4	0.5	0.1
RMSE	0.13	0.48	0.37	0.05

Note: The reference category used in this analysis is the `Difficulty = Easy` condition. Highlighted cells are those which include the contrast between the Easy condition and the Baseline condition. Note that no estimate is significantly different from zero, indicating that there is no difference between the baseline trials and the easy trials in terms of movement timing or curvature.  
+ p < 0.1, \* p < 0.05, \*\* p < 0.01, \*\*\* p < 0.001



## Appendix C: Additional figures for Chapter 4

Figure 0-1 Simulated trajectories and curvature distributions as decision boundary varied

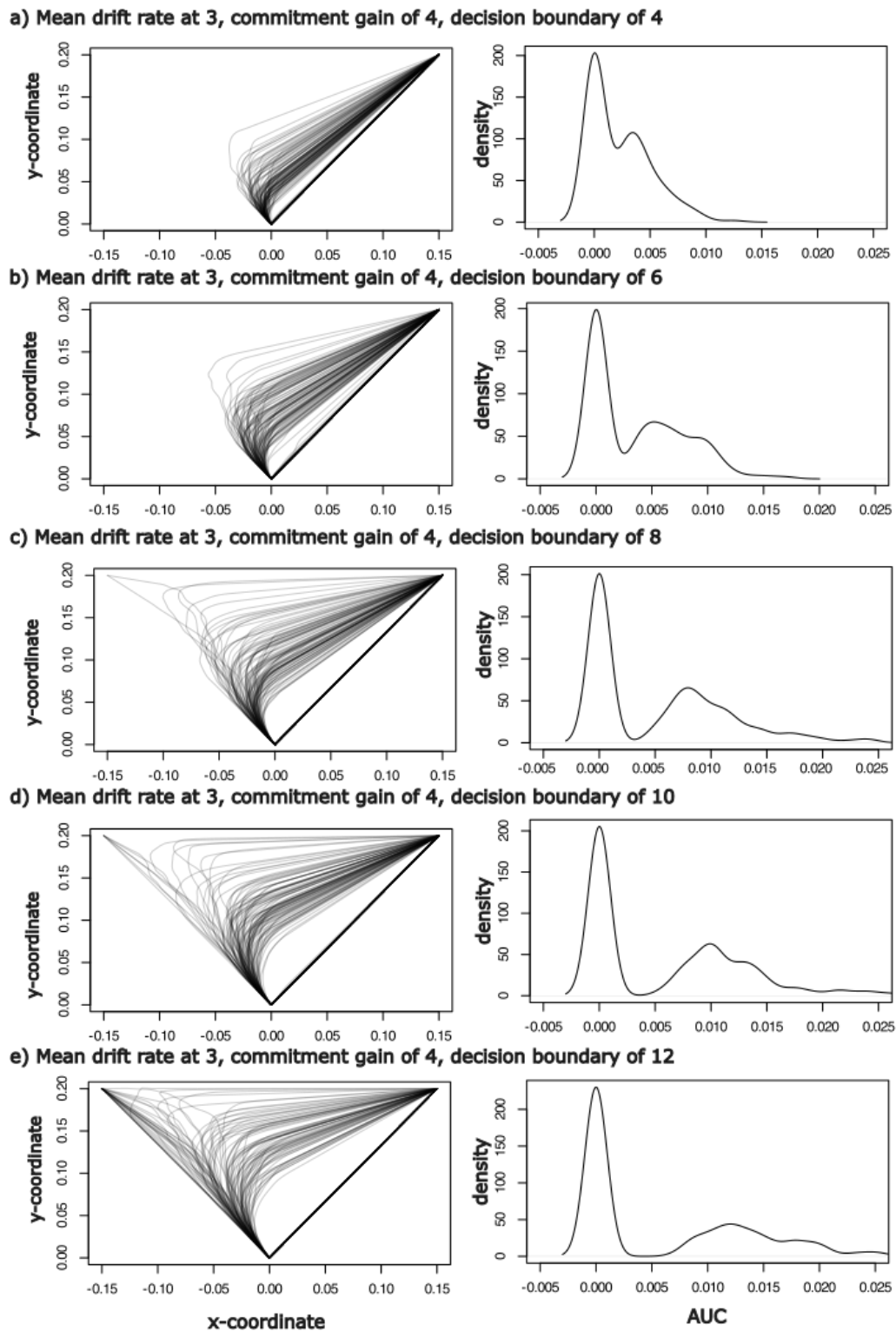


Figure 0-2 Simulated trajectories and curvature distributions as commitment gain varied

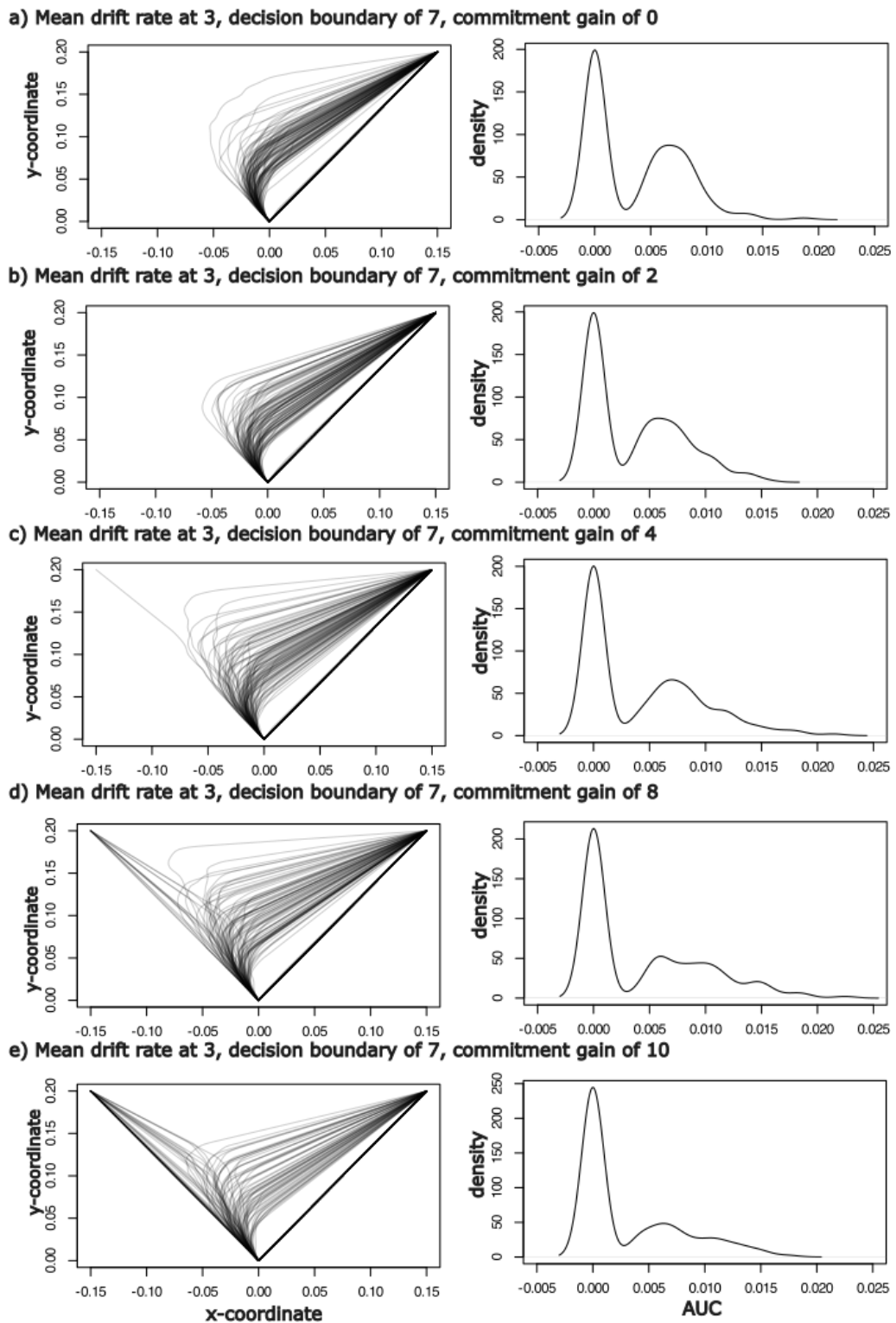


Figure 0-3 Simulated trajectories, baseline modified AUC distribution and hard choice AUC distribution for participant 1

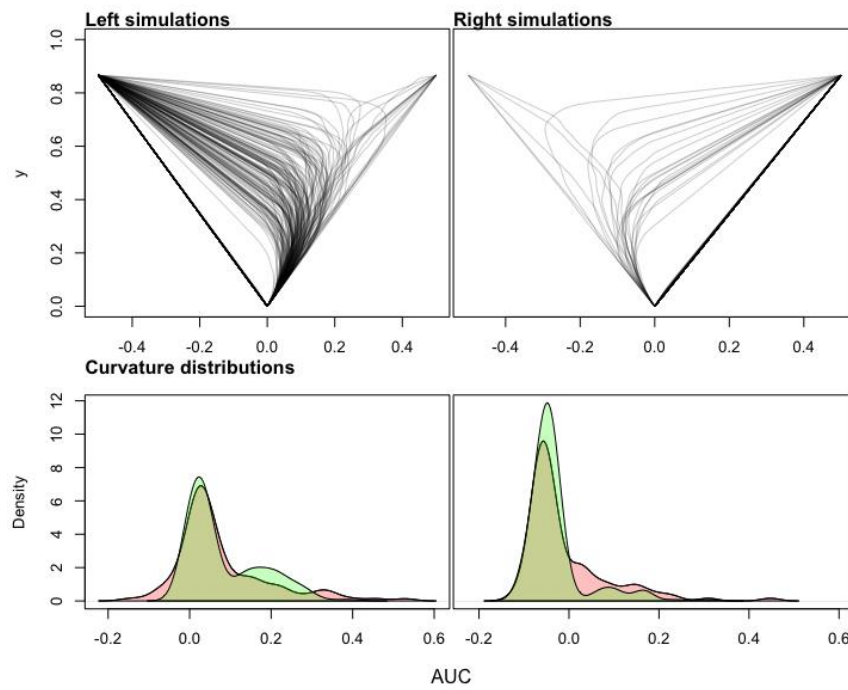


Figure 0-4 Simulated trajectories, baseline modified AUC distribution and hard choice AUC distribution for participant 2

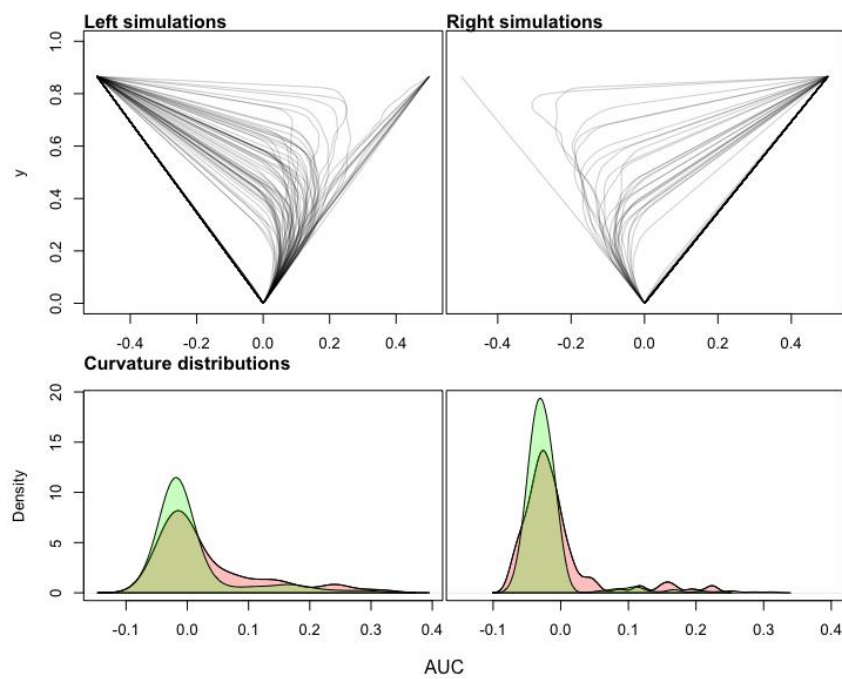


Figure 0-5 Simulated trajectories, baseline modified AUC distribution and hard choice AUC distribution for participant 3

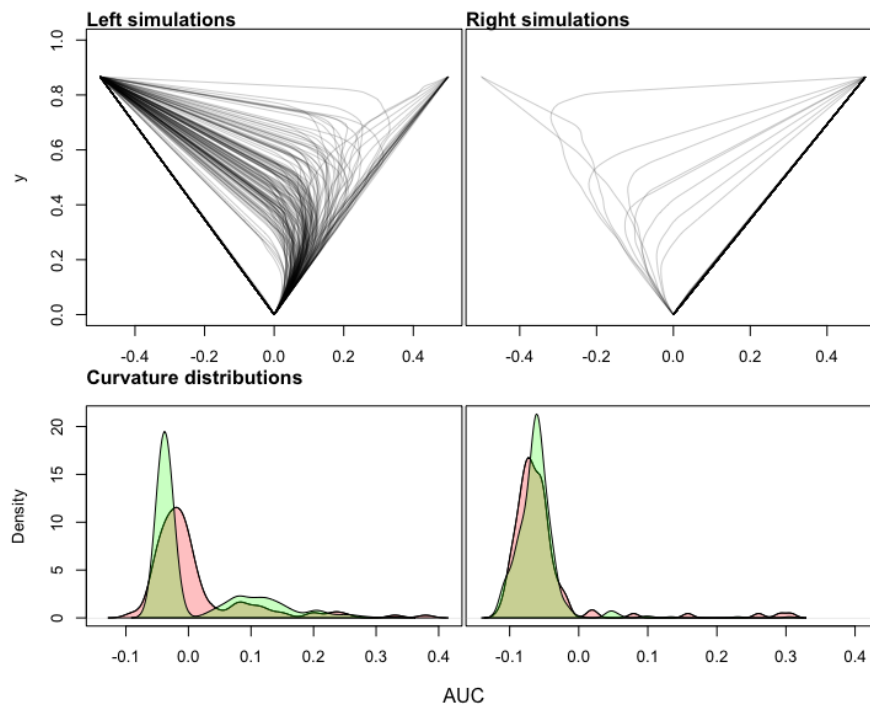


Figure 0-6 Simulated trajectories, baseline modified AUC distribution and hard choice AUC distribution for participant 4

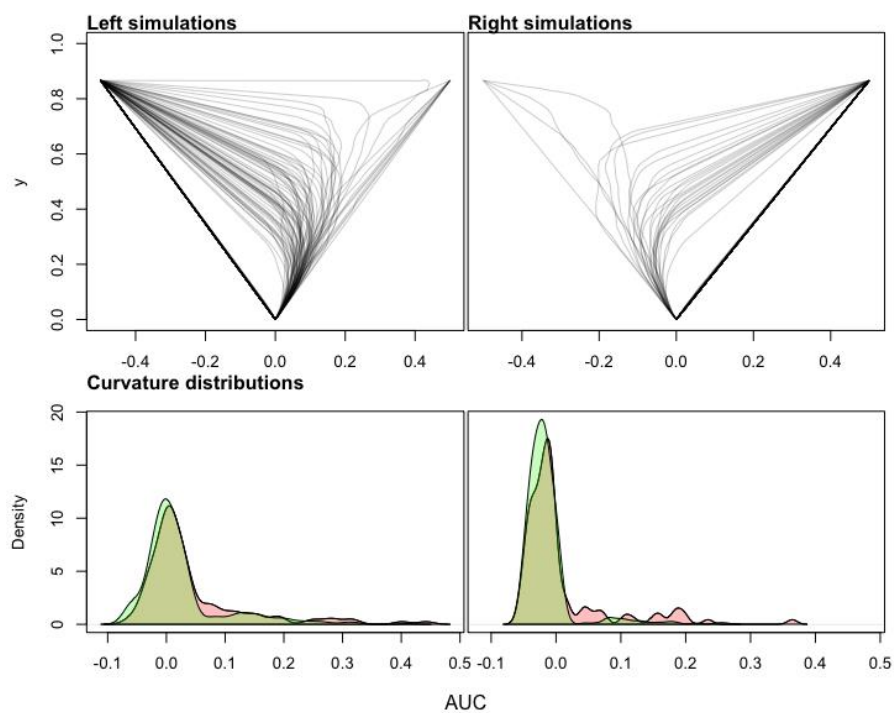


Figure 0-7 Simulated trajectories, baseline modified AUC distribution and hard choice AUC distribution for participant 5

