

Hitting the target or striking out? Timed interception, inhibitory control, and mathematics attainment in adolescents

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A published paper appears in Chapter 2 of this thesis. *Pickavance JP, Giles OT, Morehead JR, Mushtaq F, Wilkie RM, Mon-Williams M. Sensorimotor ability and inhibitory control independently predict attainment in mathematics in children and adolescents. J Neurophysiol. 2022;127(4):1026–39.* J. P. Pickavance developed the study concept. All authors contributed to the study design. O. T. Giles programmed the task. Testing and data collection were performed by J. P. Pickavance and O. T. Giles. J. P. Pickavance performed the data analysis and interpretation under the supervision of F. Mushtaq and J. R. Morehead. J. P. Pickavance drafted the manuscript, and J.R. Morehead, M. Mon-Williams, and R. M. Wilkie provided critical revisions.

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Abstract

Previous research has shown that the ability to hit moving targets is associated with children's attainment in mathematics. On the one hand, the link may result from the neural circuits that process spatiotemporal estimates being the very same that are recruited when performing mathematical operations. On the other, it may simply emerge from common control processes (most notably inhibitory control) which oversee the two. The present thesis aims to address this controversy. In the first experiment, adolescent data is combined with children's data from the interceptive task used previously, and a measure of inhibition derived from the kinematics to show the link persists through adolescence and is independent from inhibitory control. Still, recent advances have shown inhibition can be broken down into *reactive* and *proactive* components, with the suggestion *proactive* control may represent the more useful measure in applied settings. The subsequent experiment seeks to develop and test a novel task capable of providing metrics of *reactive* and *proactive* inhibition in the context of interceptive actions. Finally, this is deployed with an adolescent population to interrogate the link with mathematics. In doing so, novel insights are gained into the mechanisms underlying *proactive* control and the developmental course of interceptive timing and inhibition. In future, the highly scalable assessment developed in this thesis may help characterize and identify cognitive deficiencies in adolescents that act as barriers to their health and academic success.

Contents

Chapter 1: Introduction.....	1
1.1. Interceptive actions	2
1.1.1. Pre-programmed control	3
1.1.2. Continuous control	5
1.1.3. Hybrid control	7
1.2. Sensorimotor skills and mathematics	7
1.2.1. The shared processing hypothesis	9
1.2.2. The executive control hypothesis	11
1.2.3. Interceptive actions and mathematics	13
1.3. Inhibition	15
1.3.1. The Stop-Signal Paradigm	17
1.3.2. Proactive Inhibition	20
1.3.3. Inhibition in Adolescence	23
1.4. Overview	24
1.5. References	26
Chapter 2: Sensorimotor ability and inhibitory control independently predict attainment in mathematics in children and adolescents	34
2.1 Introduction	35
2.1.1. A shared processing account for sensorimotor skills and mathematics.....	35
2.1.2. The role of executive function for sensorimotor skill and mathematics	38
2.1.3. The present study	40
2.2. Materials and Methods	41

2.2.1. Participants	41
2.2.2. Equipment and Stimuli	42
2.2.3. Data Processing	43
2.3. Interceptive Timing and Mathematics in Adolescents	44
2.3.2. Mathematics attainment.....	44
2.3.3. Analysis	45
2.3.4. Results.....	47
2.4. The Role of Executive Control	49
2.4.1. Derivation of inhibitory control measure (false starts)	49
2.4.2. Attainment scores	52
2.4.3. Measure validation.....	52
2.4.4. Academic attainment	53
2.4.5. Results.....	54
2.4.5.1. Measure validation	54
2.4.6. Academic attainment	58
2.5. Discussion.....	62
2.6. References.....	69
2.7. Supplementary Materials	74
2.7.1. Supplement A: Interceptive timing measure validation	74
2.7.2. Supplement B: Inhibitory control measure validation	76
2.7.3. Supplement C: School Attainment Metrics	81
2.7.4. Supplement D: BRMS model specification	83
2.7.4.1. Adolescent models of mathematics attainment	84
2.7.4.2. Combined models of mathematics attainment.....	84
2.7.4.3. Combined models of English attainment	85
2.7.5. References	86

Chapter 3: Proactive inhibition of interceptive actions involves explicit changes to movement planning.....	88
3.1. Introduction	89
3.2. Results	92
3.2.1. Task performance met the assumptions of the independent race model of inhibition	92
3.2.2. Stop-signal uncertainty led to briefer movements with delays to initiation and arrival	96
3.2.3. Participants were explicitly aware of proactive changes to their movements	100
3.3. Discussion	103
3.4. Materials and Methods	109
3.4.1. Participants	109
3.4.2. Experimental Task	110
3.4.3. Procedure	113
3.4.4. Kinematic Analysis	115
3.4.5. Stop-signal Reaction Times	116
3.4.6. Proactive Inhibition.....	117
3.4.7. Model-free analysis	119
3.4.8. Reported Aim	120
3.5. References	121
3.6. Supplementary Materials.....	125
3.6.1. Supplement A: Task Instructions	125
3.6.2. Supplement B: Modelling	127
3.6.2.1. Method.....	127
3.6.2.2. Results.....	128
3.6.2.3. Individual fits	130
3.6.3. Supplement C: Context Independence Violations.....	133

Chapter 4: Reactive and proactive inhibitory control in adolescents: a cross-sectional experimental study	135
4.1. Introduction	136
4.2. Results	140
4.2.1. Adolescents met the assumptions of the independent race model of inhibition, proactively inhibited their movements, and exhibited typical behaviour in response to increased timing constraints.	140
4.2.2. Reactive inhibition had reached maturity by the onset of adolescence, whereas proactive inhibition was still developing into mid-adolescence	148
4.2.3. Participants deliberately aimed further to the rear of the target at all ages, but only adults were explicitly aware of initiation delays	150
4.2.4. Hitting performance and proactive inhibition independently predicted mathematics attainment.....	151
4.3. Discussion.....	153
4.4. Materials and Methods.....	159
4.4.1. Participants	159
4.4.2. Experimental Task and Equipment	160
4.4.3. Procedure	161
4.4.4. Kinematic Analysis.....	163
4.4.5. Stop-signal Reaction Times	165
4.4.6. Proactive Inhibition	165
4.4.7. Age related changes	166
4.4.8. Reported Aim.....	167
4.4.9. Attainment Scores	168
4.4.10. Attainment Models	169
4.5. References.....	171
Chapter 5: Discussion	175

5.1. Summary of Experimental Chapters.....	176
5.2. Limitations and Future Directions	180
5.3. Conclusion	187
5.4. References	189

List of Figures

1.1.	One degree of freedom interceptive timing task.....	5
1.2.	Location of numerical processing relative to the regions of the intraparietal sulcus involved in space and grasping.....	10
1.3.	A simple reaction time stop-signal task.....	18
1.4.	An interceptive stop-signal task.....	19
2.1.	Interceptive timing task schematic.....	43
2.2.	Marginal posterior distribution of the mathematics attainment model in adolescents.....	48
2.3.	Visualising corrected movements.....	50
2.4.	Model of interceptive timing performance.....	55
2.5.	Model of interceptive movement time.....	56
2.6.	Classifying and modelling false start movements.....	57
2.7.	Marginal posterior distribution of the mathematics attainment model.....	59
2.8.	Marginal posterior distribution of the English attainment model.....	62
2.S1.	Pairwise plots of False Start and Hit parameters.....	81
2.S2.	Attainment scores derived from standardized scores.....	83
3.1.	Interceptive stop-signal task schematic.....	93
3.2.	Empirical verification of the applicability of the independent race model.....	95
3.3.	Measures of proactive inhibition.....	99
3.4.	Spatial representation of observed timing errors and explicit reports of aiming strategies.....	102
3.S1.	Comparing the difference between stop-trial initiation times with go-trial initiations that immediately precede them.....	133
4.1.	Adapted interceptive stop-signal task schematic.....	141
4.2.	Empirical verification of the applicability of the independent race model.....	143
4.3.	Proactive changes to movements across certain and uncertain conditions.....	145

4.4. Empirical verification of Bonus Block interceptive timing performance.....	147
4.5. Age- related changes.....	149
4.6. Partial plots of the relationships between bonus targets hit percentage and proactive arrival delays, to Mathematics attainment in adolescents....	152

List of Tables

2.S1. Experimental blocks.....	78
2.S2. Attainment score conversion table.....	81
3.1. Summary statistics of measures used to calculate stop-signal reaction times.....	96
4.1. Summary statistics of measures used to calculate stop-signal reaction times for years 7, 8, and 9.....	144
4.2. Age-related change models.....	146
4.3. Best performing mathematics attainment model.....	153

Abbreviations

ADHD	Attention deficit hyperactivity disorder
CI	Confidence interval
HDPI	Highest density posterior interval
IPS	Intra-parietal sulcus
IT	Initiation time
KS2	Key-stage 2
LOOIC	Leave one out information criterion
MABC-2	Movement assessment battery for children 2
MAP	Maximum a posteriori
MT	Movement time
PFC	Pre-frontal cortex
PT	Perceptual transmission
SAT	Standardised attainment test
SNARC	Spatial-numerical association of response codes
SSD	Stop-signal delay
SSRT	Stop-signal reaction time
TE	Timing error
TT	Transmission time
TTC	Time to contact

Chapter 1: Introduction

The game of baseball is a psychological game of cat and mouse between pitcher and batter. The pitcher delivers balls the batter tries to hit. If the batter swings and misses, a strike is called; and if 3 strikes are called, the batter is out. The batter can strike out even if the pitch is un-hittable. Still, if the pitcher delivers too many unhittable balls and the batter doesn't swing, the batter gets to advance by default.

Successful batting, therefore, depends not only on the planning and execution of an accurately timed swing, but also on the ability to inhibit the swing in response to an errant pitch. In the case of hitting, it is necessary to integrate prior expectations with perceptual estimates, to plan in advance a movement of a suitable course and duration, which can then be triggered at the appropriate time to hit the ball (X. E. Brenner & Smeets, 2018; James R. Tresilian, 2005). In the case of not striking out, inhibition can be driven *reactively* in response to a stop-signal (i.e., the pitch veering off course) when it is detected early enough in the planning stages that movement can be reprogrammed or withheld entirely (Gray, 2009; Marinovic, Plooy, & Tresilian, 2009b; Nakamoto, Ikudome, Yotani, Maruyama, & Mori, 2013). Alternatively, inhibition can be driven *proactively* by delaying movement onset to maximize the chance to detect a need to stop (Aron, 2011; Verbruggen & Logan, 2009). In the present thesis, the importance of these determinants of success are considered not on the on-base percentage of elite athletes, but rather, something more universal, as neurodevelopmental

determinants of success on the journey from childhood into adulthood, through adolescence.

1.1. Interceptive actions

Our survival as a species has relied for many thousands of years on our ability to catch a moving prey or fend off an advancing attack. Whether hunting and fighting as our ancestors once did, or catching and batting in baseball today, these movements represent a class of goal-directed behaviors called *interceptive actions*. They are defined simply by the requirement that the effector's (e.g., spear's, shield's, bat's) position intersects with that of the moving target (e.g., fish, axe, ball) at the same moment in time.

The human sensorimotor system is remarkably adept at interceptive actions. Given that the average fastball clocks in at around 40m/s and must travel 18.4m, elite batters have approximately 500ms to meet the ball from its release from the pitcher's hand. Consider further that the swing itself takes approximately 250ms to reach the strike zone (E. Brenner, Driesen, & Smeets, 2014), average reaction times are of the order of 100-200ms (Jain, Bansal, Kumar, & Singh, 2015), and there are neural delays of up to 100ms inherent in the sensorimotor system (E. Brenner & Smeets, 1997; Nijhawan, 2008). Successful swings of the bat, therefore, must be initiated at the very limits of biological time.

Not only must movements be made quickly, but they must also be made precisely. A fastball may only be hittable in the "strike zone" for a millisecond or two. And yet in the face of noisy and imperfect sensory

(Faisal, Selen, & Wolpert, 2009) and motor (Franklin & Wolpert, 2011) neural transmission, elite batters are able to hit moving targets with a standard deviation of 4ms of error (referred to as precision), and the average adult human within 7ms precision (E. Brenner, van Dam, Berkhout, & Smeets, 2012). For context, that's within 1 or 2 beats of a flies wing (Deora, Singh, & Sane, 2015). This astonishing level of proficiency has spurred many programs of research to converge on the same fundamental question; how?

The underlying mechanisms remain a topic for debate, with several competing control models hypothesised. They can be broadly categorized as either *programmatic control* or *continuous control* models. Programmatic control models are entirely open loop, with the movement parameters set prior to initiating the movement. Continuous control models, on the other hand, emphasise online corrections to movements in response to visual feedback as the task unfolds.

1.1.1. *Pre-programmed control*

Tresillian's (2005) pre-programmatic control model suggests a generalised motor programme (GMP) is triggered when the time taken for the effector to reach the interceptive point (TTC_{crit}) is equal to the time taken for the target to reach the interceptive point (TTC_{tgt}). Beyond the programmed movement time of the effector (MT_{prog}), TTC_{crit} must also consider the perceptual transmission time (PT) of afferent commands from the retina to the GMP, and the transmission time (TT) of efferent commands to the effector muscles from the GMP. Accordingly, the signal to initiate movement is triggered when:

$$TTC_{tgt} = TTC_{crit} = MT_{prog} + PT + TT \quad (1)$$

Because PT and TT are fixed, control over when movement is initiated is defined by MT_{prog} . The model accommodates empirical observations from one degree of freedom (1-df) interception tasks in which target and effector movements are fixed to a single plane perpendicular to one another (e.g. Figure 1.1). Manipulations to the movement distance D , target velocity V , the length of the target L , and the width of the bat W , yield variations in observed movement times. Specifically, movement times are briefer when the target is moving faster, but longer when the width, length and distance are increased. This is summarised by the following parametric equation:

$$MT = a + \beta_1 D - \beta_2 V + \beta_3 [L + W]/V \quad (2)$$

The reduction in movement time in response to an increase in timing demands (i.e. increases in V and decreases in L and W) is adaptive, with briefer movements producing less variability in timing errors (J. R. Tresilian, Oliver, & Carroll, 2003; J. R. Tresilian, Plooy, & Carroll, 2004; James R. Tresilian & Plooy, 2006). Curiously, this is the opposite of Fitts' law, which dictates that movements requiring more spatial precision (i.e. smaller objects, further away) are longer in duration (Fitts, 1954). In the case of temporal precision, however, briefer MTs allow participants to view the target for longer, increasing the accuracy of their TTC_{tgt} prediction (RA Schmidt, 1969). They also help to minimise imprecision in the motor command. As movement times reach their minima, a practical limit is placed on one end of the distribution of the resulting movement durations, thus reducing variability in this source of error (James R. Tresilian, 2005).

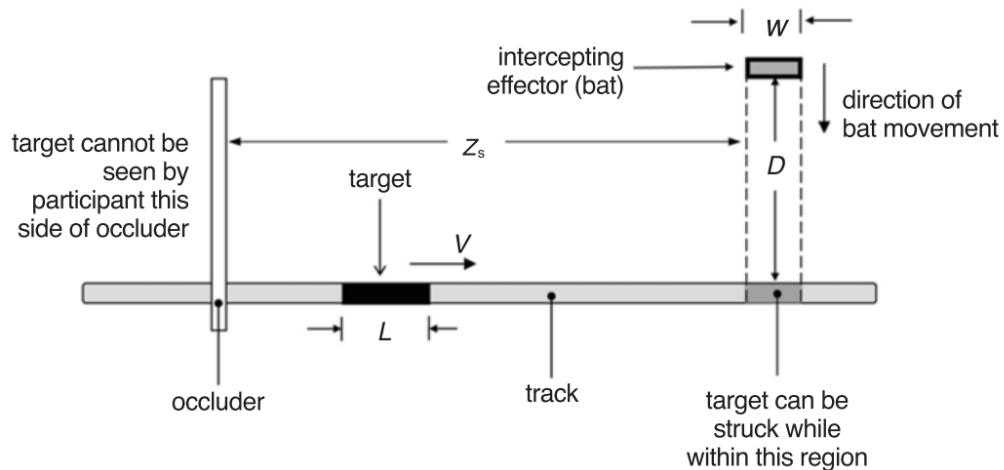


Figure 1.1. One degree of freedom interceptive timing task (reproduced from Tresillian, 2005). The target of length L moves with velocity V horizontally towards the interceptive region. A bat of width W moves a distance D perpendicular to the target in order to strike it.

1.1.2. Continuous control

There are several observations pre-programmed models fail to accommodate. Elite cricketers, for example, develop strategies to track the ball with their eyes for longer when batting (Mann, Spratford, & Abernethy, 2013). Furthermore, in non-expert populations, performance is reduced if targets are briefly occluded once the movement has been initiated (E. Brenner & Smeets, 2011), and blinks and saccades are suppressed until approximately 200ms after interceptions are made (Mrotek & Soechting, 2007). Finally, there are changes in the movement of the effector that are associated with unexpected changes in both the target's path (Paulignan, MacKenzie, Marteniuk, & Jeannerod, 1991), and the effector's position (Franklin & Wolpert, 2008). Taken together, these observations suggest the availability of visual information throughout the full duration of the target's trajectory is necessary for optimum performance.

A number of models have formalised this (e.g. Dessing, Bullock, Peper, & Beek, 2002; Peper, Bootsma, Mestre, & Bakker, 1994). For example, the required velocity model (Peper et al., 1994) states the required lateral velocity of the bat (V_b) is equal to the lateral displacement between the bat and the target ($X_t - X_b = D$) divided by the time taken for the target to reach the interceptive point (TTC_{tgt}):

$$V_b = D / TTC_{tgt} \quad (3)$$

The bat's velocity is continuously updated through the application of force as a function of the disparity between the rate of change of D and the TTC_{tgt} .

While such models can account for observations that emphasise the availability of sensory information throughout the duration of the action, there are challenges. Firstly, they imply longer movement times minimise error as this would allow finer tuning through online corrections, the opposite of what is observed when target velocity is increased (J. R. Tresilian et al., 2003). Furthermore, with sensorimotor delays estimated at about 100ms (E. Brenner & Smeets, 1997), online control alone cannot be driving behaviour in tasks with small movement times (~300ms) that require rapid responses, such as the swing of a bat.

1.1.3. Hybrid control

Neither category of model can account for all observations. Recent work, therefore, converges on a hybrid model of control (e.g., Brenner and Smeets, 2019). Under this view, predictions are made based on sensory information prior to movement, which, once initiated, is updated continuously in response to sensory information as the task unfolds. The balance between predictions and online corrections will be weighted differently depending on the specific task demands. For example, at one end of the spectrum, there is the case of catching a flyball. The catcher has plenty of time to observe the ball's trajectory and can use continuous control strategies to converge on the spot the ball will land (Fink, Foo, & Warren, 2009). Batting is at the other end of the end of the spectrum. In this case, success is almost entirely determined by integrating accurate estimates of the ball's trajectory into a swing of sufficient course and duration that they coalesce in space and time (James R. Tresilian, 2005). It is interceptive actions of the latter type that are the focus of this thesis. This is because the veracity of the perceptual estimates upon which target hitting performance lies, may hold important insights into the phylogenetic and ontogenetic development of our species.

1.2. Sensorimotor skills and mathematics

A curious feature of human development is that sensorimotor functions that are pre-established in infancy and childhood bear on cognitive functions that continue to develop through adolescence and into adulthood, such as abstract and mathematical reasoning. Indeed, it was Piaget who first

suggested the sensorimotor system provides the necessary foundations upon which higher-order cognitive abilities are built. Since then, evidence has accumulated from both typical and atypical populations supporting this view. For example, those with developmental coordination disorder tend to perform poorer in mathematics (Gomez, Piazza, Jobert, Dehaene-Lambertz, & Huron, 2017). Conversely, those with dyscalculia, a disability defined by difficulties learning arithmetic, tend to perform worse in motor tasks relative to neurotypical peers (Westendorp, Hartman, Houwen, Smith, & Visscher, 2011). More recently, in neurotypical populations of children and adolescents, the ability to hit moving targets in a 1-df interceptive timing task (i.e., Fig. 1.1) was associated with their attainment in mathematics (Giles et al., 2018). Indeed, meta-analysis indicates these links are robust in children as young as 3, all the way through to adulthood (Xie, Zhang, Chen, & Xin, 2019).

From a neurodevelopmental perspective, these associations are usually explained in one of two ways. Firstly, there is the suggestion sensorimotor and abstract mathematical processes emerge from the same cortical networks in the brain, hitherto referred to as the “shared processing” hypothesis (e.g., Anderson, 2010; Dehaene, 2004). Secondly, there is a more indirect explanation; there are executive control processes that are common between goal-directed sensorimotor tasks and abstract reasoning, because they both require adequate planning, sequencing, and monitoring, in their successful execution (e.g., Hartman, Houwen, Scherder, & Visscher, 2010; Roebbers et al., 2014).

1.2.1. The shared processing hypothesis

The history of mathematics is replete with connections between number and space, from the use of Agrand diagrams to represent complex numbers, to the exploration of high-dimensional space in the optimization of hyperparameters in machine learning. More than simply a metaphor, however, our mathematical understanding may be constrained by the very neural architecture that has given rise to it (Anderson, 2010).

These theories began to gain popularity following the simple observation that response times to numbers larger in magnitude are quicker when they are presented on the right than the left (Stanislas Dehaene, Bossini, & Giraux, 1993), dubbed the spatial-numerical association of response codes (or SNARC) effect. It was suggested numerical operations were conducted on a “mental number line” with magnitudes increasing from left to right, which requires spatial attention to be directed along the number line to perform operations (Hubbard, Piazza, Pinel, & Dehaene, 2005). Thus, evidence was beginning to emerge that the brain organised abstract constructs (i.e., magnitude of number) in concrete, physical terms (i.e., space), more commonly implicated in sensorimotor processes.

Subsequent research has identified the Intra-Parietal Sulcus (IPS) as the likely neural locus of these operations (Fig. 1.2), as it shows increased activity during both numerical (S. Dehaene, Spelke, Pinel, Stanescu, & Tsivkin, 1999) and sensorimotor operations (Andres, Michaux, & Pesenti, 2012). Indeed, more recently, the neural signature of the SNARC effect has been localized to the IPS (Cutini, Scarpa, Scatturin, Dell’Acqua, & Zorzi, 2014a).

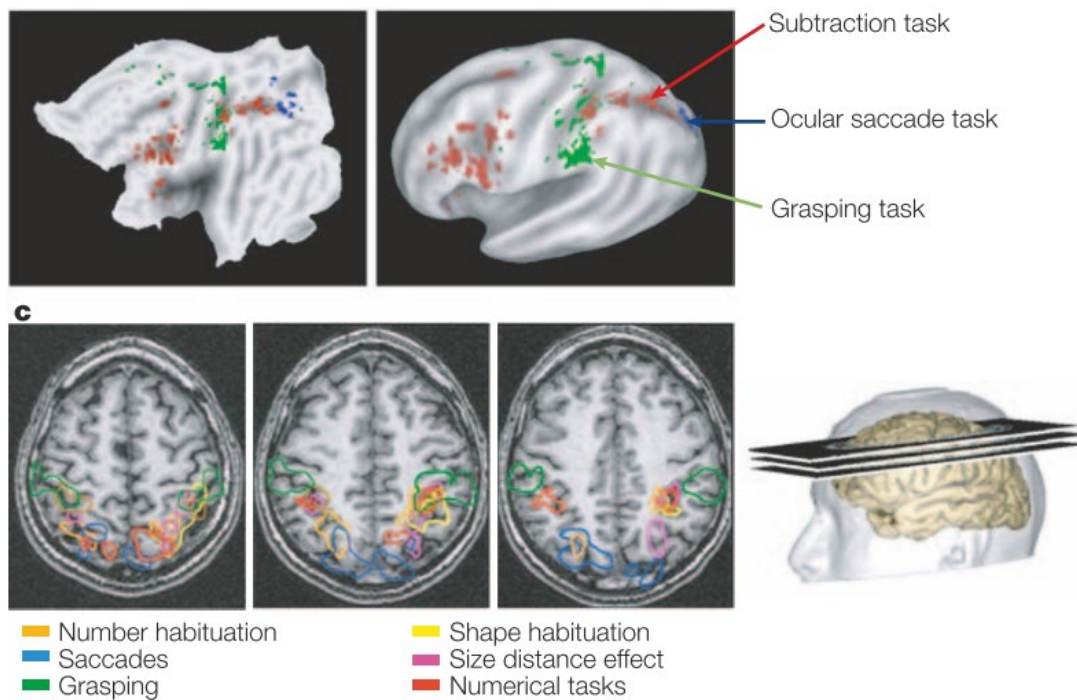


Figure 1.2. Location of numerical processing relative to the regions of the intraparietal sulcus involved in space and grasping. Coloured areas represent areas activated during different tasks. Reproduced from Hubbard et al., 2005.

Parallel strands of behavioural research further support this view. In contrast to a precise, symbolic representation of number, numerosity is the rapid “number sense” for approximating the quantity of discrete elements in an array, and is the foundation upon which mathematical operations are built (Halberda, Mazocco, & Feigenson, 2008; Starr, Libertus, & Brannon, 2013). Adaptation studies reveal that after short exposure to a dense array of dots (large numerosity), participants underestimate the numerosity of a subsequent test array (Burr & Ross, 2008). These effects appear to hold regardless of the sensory modality of the externally generated event (Arrighi, Togoli, & Burr, 2014) and can be generated internally through the motor system (Anobile, Arrighi, Togoli, & Burr, 2016). In this way, sensorimotor processes are deeply linked to mathematical operations. This work points

towards a common neural structure supporting the shared processing of sensorimotor and mathematical operations, and perhaps something more radical still; mathematical and sensorimotor processes may fundamentally be the same (Anobile, Arrighi, Castaldi, & Burr, 2020).

1.2.2. The executive control hypothesis

An alternative explanation for the link between sensorimotor skills and mathematics is that all successful operations require an adequate controller. Rather than a structural and functional overlap between sensorimotor and mathematical processes themselves, therefore, it is the executive functions overseeing these operations that are common. Executive functions are a group of correlated but distinct cognitive processes responsible for controlling and organising goal-directed behaviour (Anderson, Jacobs, and Anderson, 2008). They can be understood in terms of three core domains: *updating*, the ability to maintain relevant information in working memory; *inhibition*, the ability to suppress prepotent responses; and *shifting*, the ability to switch attention between task relevant goals (Diamond, 2013).

The coordination of these processes is tantamount to the sequencing and execution of the complex series of processes that are necessary to perform abstract linguistic (Cantin, Gnaedinger, Gallaway, Hesson-McInnis, & Hund, 2016) and mathematical operations (Bull & Scerif, 2001). Equally, the sequencing and execution of goal-directed actions depends on executive functions (Hartman et al., 2010; Luz, Rodrigues, & Cordovil, 2015; Roebbers et al., 2014). Task demands may emphasise certain domains over others. *Updating* would seem particularly important in ballet, for example, with

dancers having to maintain the correct sequence of steps in working memory as they progress through their routine. In the context of interceptive actions, *inhibition* is paramount. In catching a ball, for example, it is a fundamental requirement to withhold the planned movement until the moment at which it is necessary (Aron, 2011; James R. Tresilian, 2005). Indeed, of updating, inhibition, and shifting, only inhibition is uniquely associated with catching performance (Ludyga et al., 2019)

The executive control hypothesis posits that the link between sensorimotor skills and mathematics is indirect and mediated by domains of executive function. Indeed, many studies to date report that when measures of executive function are included in analyses of sensorimotor skill and mathematics attainment, it is executive function and not sensorimotor skill that explains the shared variance (Michel, Molihor, and Schneider, 2019; Rigoli et al., 2012; Roebbers et al., 2014; Schmidt et al., 2017; Zhang et al., 2018). Nevertheless, these studies commonly adopt the Movement ABC-2 (Henderson, Sugden, and Barnett, 2007). While reliable, it is only valid insofar as to discriminate those with movement impairments from those without, based on a crude percentile threshold of the overall score. A scalable, parametric assessment of sensorimotor skill and executive function is required to produce statistical models that are sufficient to explain the nature of these links.

1.2.3. *Interceptive actions and mathematics*

The 1-df interception task (Fig. 1.1) represents a parametric assessment of sensorimotor skill. By manipulating target speed and width, a range of timing constraints can be specified over which a parametric measure of performance can be computed as the proportion of targets hit. Recent work adopting this measure found a link with mathematics attainment (Giles et al., 2018). As discussed previously, success in this task depends on being able to integrate accurate spatiotemporal estimates into a movement of suitable amplitude and duration to coalesce with the target in time and space (X. E. Brenner & Smeets, 2018; J. R. Tresilian & Houseman, 2005). Given that perceptual estimates of space and time share the same processing architecture as magnitude and number (Anobile et al., 2020), and are implicated in arithmetic (Cutini, Scarpa, Scatturin, Dell'Acqua, & Zorzi, 2014b; S. Dehaene et al., 1999; Hubbard et al., 2005) perhaps timed interception was associated with mathematical attainment because numerical operations are deeply rooted in the same cortical networks that subserve the spatiotemporal representations necessary to successfully intercept targets.

Alternatively, the link may be explained by the proficiency of executive control processes common between the two (Hulme, 2019). *Inhibitory* control, in particular, is necessary to withhold interceptive actions until the precise moment they are required (Aron, 2011; Marinovic et al., 2009b). Similarly, inhibition is implicated in the sequencing and monitoring of processes necessary to perform mathematical operations (Bull & Scerif, 2001; St Clair-Thompson & Gathercole, 2006). Moreover, inhibitory

deficiencies are often associated with difficulties self-regulating, which can manifest as behavioural problems in class settings (Jacobson, Williford, and Pianta, 2011) with an adverse effect on learning and attainment (Gutman and Vorhaus, 2012). Perhaps, therefore, interceptive performance was related to mathematics because they both depend on the ability to organise and control goal-directed behaviours.

While Giles et al (2018) provided a parametric assessment of interceptive performance, inhibition was not considered, nor were broader measures of executive function. Accordingly, the nature of the link between interceptive actions and mathematics is still an open question. In the first experimental chapter of this thesis (Chapter 2), therefore, a crude kinematic measure of inhibition is developed from the 1-df interceptive timing task. In this way, models of mathematics attainment including parametric measures of both sensorimotor skill and inhibition can be constructed, interrogating the independence of these factors.

While clearly of theoretical interest, there are many practical implications. For example, if interceptive performance independently predicts mathematics, tests of sensorimotor control, in addition or in place of executive control, may help earlier identify children in danger of falling behind their peers in academic attainment (e.g., Michel, Molitor, and Schneider, 2019). More radically, it is conceivable that training of a sensorimotor skill could improve academic outcomes either directly by augmenting the shared circuitry (e.g., Asakawa, Murikami, and Sugimura, 2019; Erasmus et al., 2016), or indirectly by strengthening executive control processes (e.g., Westendorp et al., 2014). Finally, considering the possibility these

explanations are not mutually exclusive, such a tool may be able to tailor mathematics curricula to individuals' needs. Characterising an individual's learning difficulties in terms of sensorimotor or executive control deficiencies, for example, may indicate different avenues for intervention.

1.3. Inhibition

The measure of inhibition derived from the kinematics is defined as the proportion of trials on which the participant initiated more than 200ms prior to their mean initiation, which we assume to approximate the number of inhibition trigger failures. If this says something new about the relationship between sensorimotor skills, executive functions, and mathematical reasoning, the subsequent experimental chapters of this thesis are aimed at developing a novel task capable of producing *bona fide* metrics of inhibition in the context of interceptive actions (Chapter 3), that can be deployed in applied settings to interrogate the developmental and educational implications (Chapter 4). Still, inhibition is a broad psychological construct simply defined as the ability to withhold a prepotent response (Diamond, 2013). Unsurprisingly, therefore, there are several alternative experimental paradigms to consider in deriving a measure.

The Stroop task (Stroop, 1935), for example, requires participants to respond with the printed colour of a word. In congruent trials the print colour matches the word, whereas in incongruent trials the word will be an alternative colour. In this case, the prepotent response to the stimuli is the named word, which must be suppressed to respond with the printed colour.

The difference in response time between congruent and incongruent trials represents the latency of the inhibitory process. Similarly, anti-saccade (Munoz & Everling, 2004) and go/no go (Donders, 1969) tasks require participants to modulate responses to imperative stimuli. In the case of the former, the imperative stimulus is directional. The prepotent response is to direct gaze in the same direction. However, in incongruent trials this must be suppressed, and gaze directed in the opposite direction. Once again, inhibition is construed as the difference in response times between congruence conditions. For the latter, participants are asked to respond on a go stimulus (e.g., a real word) and suppress the response on a no-go stimulus (e.g., a fake word), with reaction times and error rates taken as measures of inhibition.

While these paradigms all purport to measure “inhibition”, it’s not clear they directly apply in the context of inhibiting interceptive actions. In the case of hitting a fastball, for example, overriding the prepotent response to swing is not arbitrarily enforced by an instruction at the outset, as in the case of Stroop or anti-saccade tasks. Moreover, while the go/no-go task appears to have more face validity, the instruction to suppress the response is still contained within the imperative stimulus. In the case of hitting a fastball, however, the early stages of hittable and unhittable balls’ trajectories may be identical, and it’s only later in flight that the paths may deviate and the instruction to withhold the response present itself. Thus, while as *de facto* measures of inhibition they are likely to correlate with the inhibitory processes underlying interceptive performance, if we are to best account for any shared variance between interceptive actions and inhibition, a measure

is required in which the signal to suppress the response is presented after the imperative stimulus.

1.3.1. The Stop-Signal Paradigm

The stop-signal paradigm (Logan & Cowan, 1984) includes inhibition tasks that fit this specification. On go trials, an imperative stimulus is presented that must be responded to as quickly as possible. On a small proportion of trials (stop trials), a stop-signal is introduced following the imperative stimulus which indicates the response should be withheld. The underlying mechanism has been conceptualized as a race between a go process which accumulates in response to the imperative stimulus, and a stop process which accumulates in response to the subsequent stop signal (Matzke, Verbruggen, & Gordon, 2020). The process which reaches threshold first wins the race and determines the outcome, which appears to be recapitulated in electrophysiological recordings from the basal ganglia (Robert Schmidt et al., 2013). Necessarily, the stop process is faster than the go process, otherwise movement would never be inhibited. By staircasing the delay at which the stop signal is presented, the latency of the stop process, or the time prior to initiation when an individual can correctly inhibit their movement in response to the stop signal 50% of the time, can be determined by subtracting the mean stop signal delay from the mean reaction time on go trials (Fig. 1.3; Verbruggen et al., 2019). This, the stop-signal reaction time (SSRT), is the primary measure of reactive motor inhibition.

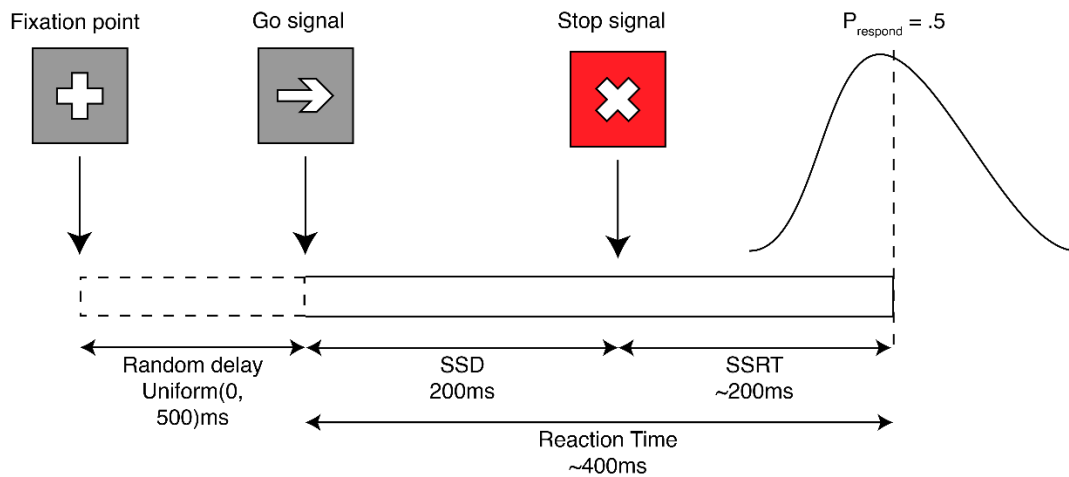


Figure 1.3. A simple reaction time stop-signal task. (Left to right) The go signal appears after a random delay which must be responded to correctly (i.e., with the corresponding character) as quickly as possible. On stop-trials, a stop signal is presented after the imperative stimulus at a staircased delay, the stop signal delay (SSD). Over the course of many trials, the point at which movements are inhibited 50% of the time is reached and the stop-signal reaction time (SSRT) can be calculated by subtracting the mean SSD from the mean reaction time on go trials.

Stop-signal reaction times have been recorded in several response paradigms including simple reaction time tasks (e.g., Li, Huang, Constable, & Sinha, 2006; Logan & Cowan, 1984), choice reaction tasks (e.g., Rae et al., 2018; Senderecka, Grabowska, Szewczyk, Gerc, & Chmylak, 2012), and anticipation timing tasks (e.g., Coxon, Stinear, & Byblow, 2006; Slater-Hammel, 1960; Vink et al., 2005). SSRTs vary depending on the complexity of the task, from about 150ms to 220ms (Leunissen, Zandbelt, Potocanac, Swinnen, & Coxon, 2017). They have been critical to understanding and treating of a range of neuropathologies because they are often elevated in conditions characterized by inhibitory deficiencies such as attention deficit/hyperactivity disorder (Dimoska, Johnstone, Barry, & Clarke, 2003;

Lijffijt, Kenemans, Verbaten, & Van Engeland, 2005; Van Hulst et al., 2018), addiction (Smith, Mattick, Jamadar, & Iredale, 2014), and obsessive-compulsive disorders (Lei et al., 2015). Similarly, SSRT has been linked with mathematical attainment, with better inhibitory performance associated with improved arithmetic (St Clair-Thompson & Gathercole, 2006).

Stop-signal reaction times have also been reported in the context of a 1-df interception task (Marinovic, Plooy, & Tresilian, 2009a). Under this scheme, TTC_{crit} is analogous to the moment the imperative stimulus would be presented in a simple reaction time task (i.e., the triggering of the go process), with the stop-signal presented at a staircased delay afterwards (Fig. 1.4). Critically, participants must be trained to move at a certain movement time prior to experimental blocks to ensure the stop signal delay is yoked to TTC_{crit} . This study, and others like it, confirms that inhibition is broadly equivalent between interceptive and other stop-signal response paradigms (Gray, 2009; Marinovic et al., 2009b; Nakamoto et al., 2013). In principle, therefore, it is possible to measure reactive inhibition in the context of interceptive actions using the stop-signal paradigm as applied to a 1-df interceptive task.

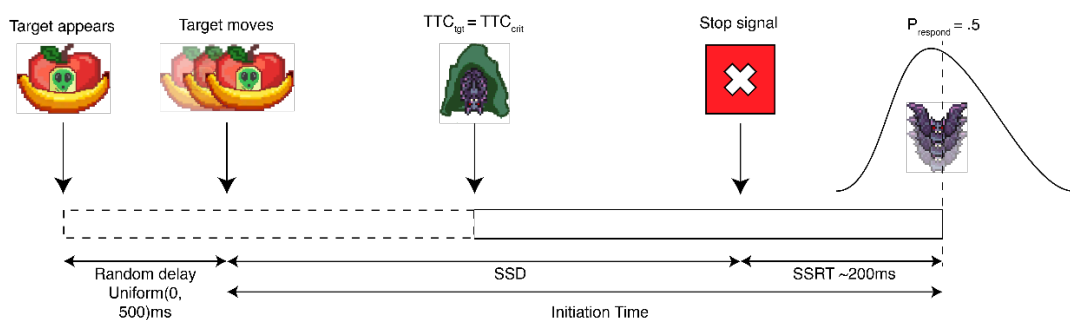


Figure 1.4. An interceptive stop-signal task. (Left to right) The target begins to move after a random delay at a fixed speed. On go trials, the GMP is triggered at TTC_{crit} .

On stop-trials, a stop signal is presented after TTC_{crit} at a staircased delay (the SSD). Over the course of many trials, the point at which movements are inhibited 50% of the time is reached and the stop-signal reaction time (SSRT) can be calculated by subtracting the mean SSD from the mean initiation time on go trials.

1.3.2. *Proactive Inhibition*

Recent work, however, reveals stop-signal reaction times are not the only signature of inhibition in the stop-signal paradigm. A curious observation commonly made is that participants delay their go response under the uncertainty of whether a stop-signal will be presented (Jahfari et al., 2012; Verbruggen & Logan, 2009; Vink et al., 2005, 2014), with greater delays associated with an increased probability and expectation of stop signals (Vink, Kaldewaij, Zandbelt, Pas, & du Plessis, 2015). In contrast to the latency of the automatic, *reactive* process measured by SSRT, this shift is thought to be a volitional, *proactive* strategy that improves the probability of correctly inhibiting in response to the stop-signal by permitting more time to detect it.

The suggestion proactive inhibition is a volitional and strategic adjustment has led to speculation it may represent the more ecological domain. For example, an addict's substance avoidance or the suppression of a child's tics is unlikely to recruit reactive mechanisms in response to external stimuli, but may depend rather on the ability to delay their expression (Aron, 2011). Likewise, in the case of the sequencing and performing of mathematical operations, and in the self-regulatory maintenance of goals, it would seem volitional, proactive strategies have more face validity. Nevertheless, while research is beginning to emerge that distinguishes between deficits in reactive and proactive inhibition in clinical

contexts (e.g., Van Hulst et al., 2018), studies have yet to re-examine the links between inhibition and educational outcomes under this reconceptualization. Rather than simply replicate the previous 1-df interceptive stop-signal task (Marinovic et al., 2009a), therefore, a novel interception task is indicated. By experimentally manipulating the certainty a stop-signal may be presented; delays to initiation and arrival, and differences in movement time, provide valuable metrics of proactive inhibition, in addition to SSRT. Not only does this promise to improve our predictive models of mathematics, but it will also, for the first time, characterize precisely the inhibitory deficiencies associated with poorer academic outcomes.

While a task producing metrics of interceptive performance, and reactive and proactive inhibition in the context of interceptive actions, is required to address the central question of this thesis, such a task may also help resolve a few open questions in the realm of inhibition. Firstly, there is some debate as to how proactive inhibition is implemented. On the one hand, proactive inhibition has been modelled as an increase in the process completion threshold (Cai, Oldenkamp, & Aron, 2011; Verbruggen & Logan, 2009; Zandbelt, Bloemendaal, Neggers, Kahn, & Vink, 2013). Accordingly, the go and stop processes that are racing must reach a greater amplitude before the outcome is determined. While the threshold is increased for both go and stop processes, it is effectively ‘response suppression’ of the go process because it gives the faster stop process more time to out race it. Alternatively, proactive inhibition may simply reflect delayed facilitation of the response, or a “waiting strategy” (MacLeod, Dodd, Sheard, Wilson, & Bibi, 2003; Rieger & Gauggel, 2002).

The ability to resolve between these competing hypotheses has, to date, been constrained by utilising simple button press tasks in which response delay is the only signature of proactive inhibition. By considering inhibitory control in the planning and execution of more sophisticated behaviors, such as the swing of a bat in a 1-df task, however, it may be possible to tease apart the underlying mechanisms. Recall, the pre-programmatic model of control states movement times are programmed in advance based on the required precision, and triggered when estimates of the time taken for the target to reach the interception point are equivalent (plus neurophysiological delays)(James R. Tresilian, 2005). According to this scheme, if the triggering of the prepared response is suppressed (i.e., takes longer to complete), the prepared movement time will be inappropriate to preserve timing error and arrival to the target will be delayed. Alternatively, any delays in facilitation should be offset by a proportional reduction in movement time because movement time is specified immediately prior to triggering and can be programmed to reflect this wait. Therefore, comparing timing errors and movement times between stop-signal certainty conditions, it should be possible to resolve between these competing hypotheses.

The second question concerns the extent to which these adjustments are volitional. While proactive control is commonly characterized as an intentional strategy, this has only been assessed indirectly (Verbruggen & Logan, 2008). In motor learning paradigms, however, the extent to which behaviour is considered volitional can be directly assessed using self-reported aiming assays (Bond & Taylor, 2015; Morehead, Taylor, Parvin, & Ivry, 2017). A 1-df interception task lends itself well to this job because the

timing characteristics can be expressed spatially. Therefore, including a self-reported spatial assay of where the target was when movement was initiated, and where on the target they struck, it may be possible to assess the extent to which *proactive* strategies are governed by volitional processes.

1.3.3. *Inhibition in Adolescence*

Finally, such a task may also help to bridge the gap between neurological, observational, and experimental findings in inhibition studies with adolescents. Adolescence is a period of intense transition often characterised by heightened risk-taking and recklessness (Steinberg, 2008), which is thought to reflect deficiencies in inhibitory control of behaviour (Casey, Jones, & Hare, 2008). Imaging studies have shown this corresponds to a profound reorganization of the brain. Indeed, it is thought that the relative immaturity of the prefrontal cortex through the mid stages of adolescence explains self-regulation difficulties (Jacobson, Williford, & Pianta, 2011) and adolescent risk-taking behaviour (Blakemore & Choudhury, 2006; Konrad, Firk, & Uhlhaas, 2013; Van Duijvenvoorde et al., 2015).

Nevertheless, measures of Stroop (Leon-Carrion, García-Orza, & Pérez-Santamaría, 2004), anti-saccade (Luna, Garver, Urban, Lazar, & Sweeney, 2004), go/no go (Tamm, Menon, & Reiss, 2002), and stop-signal (Dupuis et al., 2019) performance do not follow this trajectory, with adult levels reached by the onset of adolescence. The lack of measures capable of capturing observed symptomology and neurobiological change is unfortunate. The risk-taking behaviors that emerge in mid-adolescence can

be life altering and are often associated with poor outcomes (Gutman & Vorhaus, 2012; Kipping, Campbell, MacArthur, Gunnell, & Hickman, 2012).

One explanation is that these measures only capture *reactive* processes. *Proactive* processes in other domains of control, however, have been shown to emerge later (Braver, 2012). By comparing adolescent and adult *proactive* inhibition with the 1-df stop-signal task, it is possible to determine whether this domain of inhibition continues to develop through adolescence. This could resolve the apparent contradiction between experimental measures of inhibitory control, and neurological and epidemiological observations, further providing recommendations for which measures of inhibition should be routinely included in longitudinal studies with adolescent populations.

1.4. Overview

This thesis aims to examine the basis of putative links between interceptive performance, executive functions, and attainment in mathematics. In the first experimental chapter (Chapter 2), *de novo* adolescent data is combined with data previously collected with children using a 1-df interception task (Giles et al., 2018). Using a kinematic measure of inhibition derived from trials on which “false-start” movements were made, models of mathematical attainment including both interceptive performance and inhibition as predictors are presented.

Having found interceptive performance and the proxy measure of inhibition independently predict maths attainment, the second experimental

chapter (Chapter 3) aims to develop a novel task capable of producing *bona fide* metrics of reactive (i.e., SSRT) and proactive inhibition in the context of interceptive actions. The primary goal was to empirically verify the validity of the task using an adult population. Nevertheless, comparing movement characteristics and self-reported aiming assays between conditions in which stop-signals could and couldn't appear, theoretical questions concerning the mechanisms of proactive inhibition and the degree to which it is under volitional control are also addressed.

The third experimental chapter (Chapter 4) assesses adolescents (ages 11-14) and adults with an adapted version of the novel 1-df interceptive stop-signal task developed in the previous chapter. For the first time, the development of proactive inhibition through to mid-adolescence is considered, with a view to resolve the apparent contradiction between experimental measures of inhibition and how adolescent development is characterised both neurologically and symptomatologically. In addition, bonus blocks capable of assessing interceptive timing performance over a range of timing constraints were also interleaved. Subsequently, models of mathematical attainment including parametric assessments of interceptive performance and reactive and proactive domains of inhibition are constructed. In this way, the domain(s) of inhibition relevant in an educational context is(are) identified. Finally, these models can conclusively resolve whether associations between sensorimotor and mathematical performance are engendered by shared cortical processing, or control systems common between the two.

The concluding chapter (Chapter 5) reviews the experimental findings from the previous chapters, considering their contributions in the context of limitations, with recommendations for future studies.

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Chapter 2: Sensorimotor ability and inhibitory control independently predict attainment in mathematics in children and adolescents

We previously linked interceptive timing performance to mathematics attainment in 5–11-year-old children, which we attributed to the neural overlap between spatiotemporal and numerical operations. This explanation implies the relationship should persist through the teenage years. Here, we replicated this finding in adolescents ($n = 200$, 11–15 years). However, an alternative explanation is that sensorimotor proficiency and academic attainment are both consequences of executive function. To assess this competing hypothesis, we developed a measure of a core executive function, inhibitory control, from the kinematic data. We combined our new adolescent data with the original children's data (total $n = 568$), performing a novel analysis controlling for our marker of executive function. We found the relationship between mathematics and interceptive timing persisted at all ages. These results suggest a distinct functional link between interceptive timing and mathematics that operates independently of our measure of executive function.

Keywords: Sensorimotor control, Inhibition, Academic attainment,
Mathematics

New and Noteworthy

Previous research downplays the role of sensorimotor skills in the development of higher order cognitive domains such as mathematics: using inadequate sensorimotor measures, differences in ‘executive function’ account for any shared variance. Utilizing a high-resolution, kinematic measure of a sensorimotor skill previously linked to mathematics attainment, we show that inhibitory control alone cannot account for this relationship. The practical implication is that the development of children’s sensorimotor skills must be considered in their intellectual development.

2.1 Introduction

A functional link between the development of sensorimotor skills and abstract domains of cognition has long been postulated. It was Piaget (1) who first suggested the sensorimotor system provides the necessary foundations upon which higher order cognitive abilities are built. More recently, neurobiological models of brain organization have been postulated in which neural circuits for fundamental sensorimotor processes are exapted for later emerging abstract processes such as language and mathematics (2-5).

2.1.1. A shared processing account for sensorimotor skills and mathematics

The association between spatial ability and mathematics has been studied extensively, with a recent meta-analysis finding robust effects in children as young as 3, through to adulthood (6). Perhaps this should come as no

surprise, the history of mathematics is replete with connections between number and space, from the use of Agrand diagrams to represent complex numbers, to the exploration of high-dimensional space in the optimization of hyperparameters in machine learning. More than simply a metaphor, our mathematical understanding may be constrained by the very neural architecture that has given rise to it (2).

Behavioral and neuroimaging studies are consistent with this theory. For example, response times to numbers larger in magnitude are quicker when they are presented on the right than the left (7), the so-called SNARC effect. It has been suggested numerical operations are conducted on a “mental number line” with magnitudes increasing from left to right, which requires spatial attention to be directed along the number line to perform operations (8). The Intra-Parietal Sulcus (IPS) is likely the neural locus of these operations, as it shows increased activity during both numerical (9) and sensorimotor operations (10). More recently, the neural signature of the SNARC effect has been localized to the IPS (11). This convergence of behavioral and imaging data points towards a structure supporting the shared processing of sensorimotor and mathematical operations.

Research into numerosity perception supports this view. In contrast to a precise, symbolic representation of number, numerosity is the rapid “number sense” for approximating the quantity of discrete elements in an array. It is present as early 6 months (12) and is thought to be the precursor to formal mathematical acquisition (13-14). Adaptation studies reveal that after short exposure to a dense array of dots (large numerosity), participants underestimate the numerosity of a subsequent test array (15). These effects

appear to hold regardless of the sensory modality of the externally generated event (16) and can be generated internally through the motor system (17).

Numerosity, the perceptual property that lays the foundation for mathematical processing, can therefore be thought of as a generalized sense of number that arises from sensorimotor processes (18).

We previously found children's ability to hit moving targets predicted their mathematics attainment (19). We reasoned successful interceptive timing relies on internal models of the spatiotemporal properties of the target and effector. Put simply, one must incorporate accurate estimates of the time taken for both the target and effector to reach the point of interception into a movement that is initiated at this critical time (20). Given that spatial and temporal representations may be indistinguishable (21-22), we should expect similar functional links to exist between mathematical and temporal representations (19, 22) as between mathematical and spatial representations (6). Thus, the "shared processing" hypothesis predicts interceptive timing performance should be associated with mathematical attainment because numerical operations emerge from the same cortical networks that subserve the internal models necessary to successfully intercept targets.

2.1.2. *The role of executive function for sensorimotor skill and mathematics*

It has been objected that the link between interceptive timing performance and mathematics is not a genuine functional link. Rather, it may simply reflect a common role for executive function in both contexts (23). There are three core domains of executive function: *updating*; *inhibition*; and *shifting* (24-25). Conceptualized as a cognitive veto, they have been linked to sensorimotor skills (26) and academic attainment (27-29).

Considering interceptive timing, we would expect inhibition to explain the largest amount of shared variance with academic attainment. In catching a ball, for example, it is a requirement to withhold the planned movement until necessary (30, 20). That is of course, providing enough time has elapsed to detect the target's motion and plan the corresponding movement. Allowing 200ms for detection (31) and 200ms for preparation (32), this will be the case in all but the most extreme circumstances. Moreover, previous trials strongly influence subsequent trials' timing characteristics (33), so the inhibition of prepotent responses when the target's trajectory is slower than expected is a necessary condition for success; a phenomenon exploited by the *changeup* pitch in baseball. Indeed, of the three domains, only inhibition is uniquely associated with catching performance (34).

There are two levels at which inhibitory control influences academic attainment. Firstly, the general coordination of updating, inhibition and shifting is tantamount to the sequencing and execution of the complex series of actions necessary to perform linguistic (30) and mathematical operations (28). Secondly, and more specifically, deficient inhibitory control is

associated with difficulties in self-regulating, which can manifest as behavioral problems in class settings (35) with an adverse effect on learning and attainment (36). For example, responding before the task is understood, answering before sufficient information is available, or failing to correct obviously inappropriate responses (37).

Given that inhibitory control underlies the successful interception of targets and mathematical attainment, perhaps executive control, and not shared processing, explains the association (23). This is supported by previous research in which the link between sensorimotor skills and academic attainment is extinguished when measures of executive function have been controlled for (38-42). We do not however, believe that this is sufficient to rule out the shared processing hypothesis. It is possible for interceptive timing and mathematics to share the same neural circuitry, and for independent executive control to operate between for both tasks.

If the only neural circuitry common between interceptive actions and mathematical processing involves inhibiting inappropriate responses, then an assessment of interceptive timing skills will merely assess their executive functions. An alternative account is that there is both shared processing for mathematics and sensorimotor skill, and, independently, a role for inhibitory control in both domains.

2.1.3. *The present study*

The present study addresses whether the link between interceptive timing and mathematics is independent from executive control. Firstly, we replicated our original study of children (ages 5-11) (19) in a population of adolescents (ages 11-15). We reasoned that if the relationship can be explained entirely in terms of executive functions, we would expect to see it diminished in teenagers because executive functions contribute more to successful motor performance earlier in development (43). Alternatively, if shared circuitry contributes beyond executive control, interceptive timing performance and mathematics attainment should still correlate because the link between spatial and numerical ability persists from children as young as 3 through to adulthood (6).

Having confirmed the relationship persisted in our adolescent population, we subsequently combined these new data with our previous data from school children (ages 5-11; 19) to confirm it was age invariant. Additionally, from the kinematics we derived a measure of the executive function we expect to explain the most shared variance, inhibitory control, to determine unambiguously whether these relationships operated independently. Further still, we considered a model of English attainment. We reasoned that if any independent relationship between interceptive timing and mathematics was a direct consequence of shared processing, it should not be observed with English attainment. This is because the integration of spatiotemporal estimates into timed reaching movements utilizes circuitry implicated in the processing of numerical and not linguistic representations.

2.2. Materials and Methods

2.2.1. *Participants*

For the adolescent data, two hundred participants were recruited from a secondary state school in the City of Bradford, UK. Fifty students from academic years 7 (ages 11-12 years), 8 (ages 12-13 years), 9 (ages 13-14 years), and 10 (ages 14-15 years), were selected at random to participate. The sample size was determined to yield approximately the same number of participants in each year as our previous study in which the link was originally established (19). Forty-one participants were removed because they had incomplete or out-of-date attainment records. Thus, our final adolescent sample comprised 159 participants.

The primary school and adult data were previously collected in 2017 (Giles et al., 2018). The school children were recruited from a Bradford state primary school. All primary pupils were invited to participate, with 368 from academic years 1 (ages 5-6 years), 2 (ages 6-7 years), 3 (ages 7-8 years), 4 (ages 8-9 years), 5 (ages 9-10 years), and 6 (ages 10-11 years). In addition, we recruited a cohort of adult aged participants from the University of Leeds ($n = 22$, 15 female, $\text{Mean}_{\text{age}} = 24.76$, $\text{SD}_{\text{age}} = 4.70$). Twelve participants were removed from the primary school cohort; eleven were identified as having special educational needs and one had incomplete task data.

All assessments were conducted in a private room provided by the school. All participants provided written and informed consent and did not receive compensation for their time. This study was approved by the School of Psychology Ethics Committee at the University of Leeds.

2.2.2. Equipment and Stimuli

Participants completed a computerized interceptive timing task. Using a rail-mounted manipulandum, they had to hit targets of three different speeds (levels: 250mm/s; 400mm/s; 550mm/s) and three different widths (levels: 30mm; 40mm; 50mm), with 9 combinations over 54 trials. The manipulandum was tethered to a linear potentiometer. The displacement was proportional to the change in voltage sampled at 500Hz using a National Instruments DAQ (NI-DAQ) device. All stimuli were displayed on a BenQ XL2720Z gaming monitor (598 x 336mm, 1920x1080p) at 144Hz. The task logic and stimuli were programmed in Python (version 2.7.9) by author OTG. The equipment, stimuli, and procedure were identical to those used in the original study (Fig. 2.1 and Giles et al., 2018 for further details) and can be found in an online repository along with all data and models:

<https://osf.io/yq2r5/>.

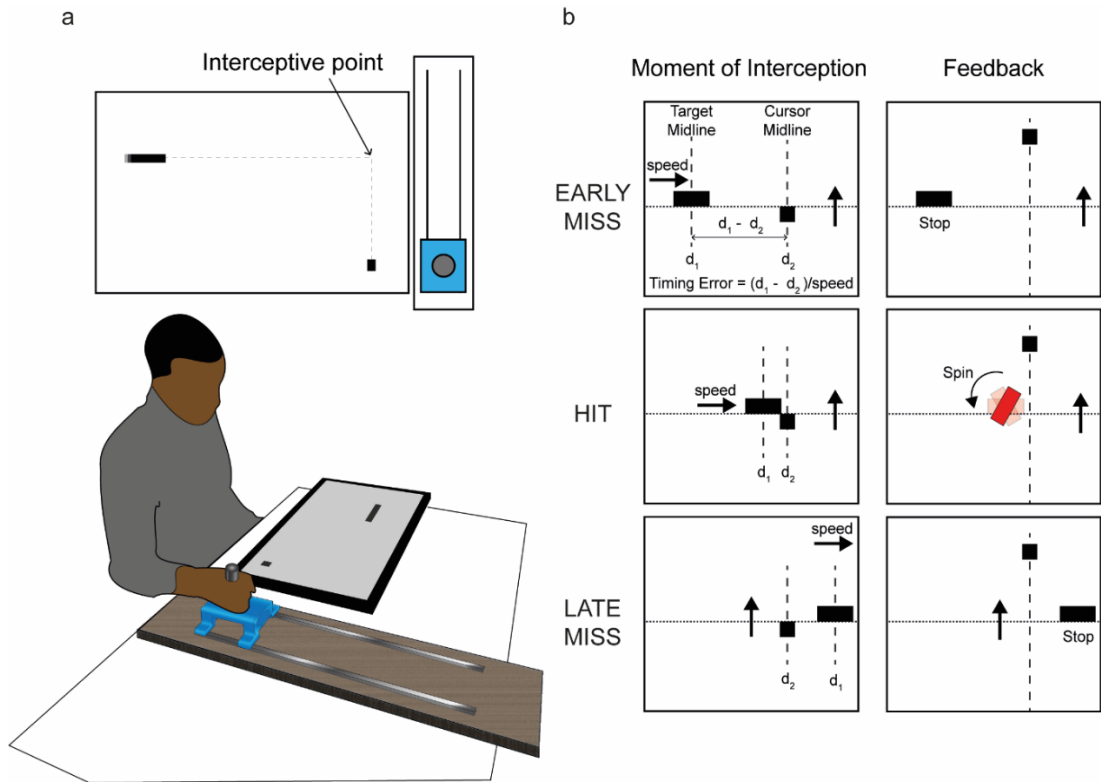


Figure 2.1. Task schematic. a) Participants were instructed to hit targets with 9 different combinations of speed and width using a rail mounted manipulandum constraining movement to 1 degree of freedom. b) Examples of Early (top), Hit (middle), and Late (bottom) errors. Interception (left) is the instance the cursor reaches the interceptive point, with the upper edge of the cursor meeting the plane continuous with the lower edge of the bat. The timing error is calculated as the displacement between the center of the target and the bat, divided by the target speed. Feedback (right) depicts the feedback given. On misses (i.e. top and bottom) the target stops the moment the cursor crosses the interceptive point. On hits the target turns red and spins anti-clockwise.

2.2.3. Data Processing

All analyses were conducted after experimental data had been collected. The position time series from each trial was filtered using a zero-lag, 2nd order, low-pass Butterworth filter with 10Hz cutoff. The initiation time was the first time the cursor's speed exceeded 40mm/s. The movement time was the time elapsed from the initiation time to the point at which the bat crossed the

interceptive plane. We used cubic interpolation on all positions of the center of the target and the center of the bat, from initiation time until maximum movement amplitude, to estimate the precise moment the bat's center intersected the interceptive plane. Hits were awarded if the difference between the position of the target and bat was less than half the sum of the width of the target and bat. Subsequently, the *proportion of targets hit* by each participant was found by dividing the number of targets hit by the total number of trials.

2.3. Interceptive Timing and Mathematics in Adolescents

Firstly, we considered whether the relationship between interceptive timing and mathematics persisted into adolescence.

2.3.2. Mathematics attainment

We used standardized attainment scores assigned by subject teachers in mathematics. These scores were awarded based on recent classwork and internal assessment and were aligned with the UK national curriculum scale (range 1-9). Teachers further discriminate ability by dividing each level into three tiers (low, middle, high). In our models, therefore, mathematics attainment is considered an ordinal variable ranging from 1-27.

2.3.3. Analysis

As academic progress is more closely aligned to year group than absolute age, participant age was grouped by academic year rather than chronological age. Furthermore, considering year group as an ordinal term may lead to overfitting and preclude examining interaction effects (44). Thus, year group was centered around the median and considered a continuous measure so that each increment was proportionally equivalent. For years 7-10, our centered age ranged from -1.5 to 1.5, with single unit increments.

The proportion of targets hit by each participant was standardized as a z-score (mean = 0, sd =1). There were five students who recorded a higher attainment score than 15 in mathematics (scores: 18, 19, 21, 21, 24). To ensure levels were not underpopulated, they were grouped into the nearest rounded mean level (score = 21).

A saturated ordinal logistic regression model was constructed to predict mathematics attainment from all plausible combinations of predictors, including an interaction between age and task performance. We additionally included gender to improve our estimates because girls tend to outperform boys academically (45) and boys performed better on the interception task in our earlier data (19):

$$Mathematics_i \sim Ordered(p)$$

$$\text{logit}(p_k) = \alpha_k + \beta_{year}Year_i + \beta_{gender}Gender_i + \beta_{hit}Hit_i + \beta_{year\beta_{hit}}Year_iHit_i$$

Parameters were estimated by Bayesian estimation, using a No-U-Turn Sample algorithm as implemented in the *brms*(ver. 2.9.0) package for R

(ver. 3.6.0), with two chains performing 1000 warmups followed by 2000 iterations (44). To ensure our estimates were conservative, all parameters were assigned weakly informative priors (Normal[0, 1]). Chains were visually examined to ensure they converged. The procedure was then used to fit models in which parameters were systematically eliminated. The final model, a null model, contained only intercepts for each level of outcome. The best model was selected by applying the Leave One Out Information Criterion (LOOIC). Comparative weights were then derived from the LOOIC. The model with the greatest weight was considered the best fitting, most parsimonious model considered (44).

The posterior distribution of the best performing model was then inspected. Parameters with a non-zero spanning 95% highest density posterior interval (HDPI) were considered significant. For significant parameters, the *maximum a posteriori* (MAP) value was interpreted as a point estimate of the mean parameter value. We could not directly interpret the effect size of parameters as the model employed a cumulative log-odds link function, which computed the log odds of an observation yielding an outcome $\leq k$, where k is each possible level of outcome. Therefore, to quantify how changes in predictors influence mathematics attainment, mean outcome values were estimated from 1000 samples of the posterior distribution, using the observed range of the predictor(s) of interest, while holding all other predictors at their mean value (46).

2.3.4. Results

One-hundred and fifty-nine adolescents performed interceptive actions in a computerized task over a range of different target speeds and sizes. We found the number of targets they hit predicted their mathematics attainment independently of their age and gender. Considering all combinations of predictors in models for mathematics, the best performing model (minimum LOOIC, maximum weight) contained year group, gender and proportion of targets hit, with no interaction effects:

$$\begin{aligned} \text{Mathematics}_i &\sim \text{Ordered}(p) \\ \text{logit}(p_k) &= \alpha_k + \beta_{\text{year}} \text{Year}_i + \beta_{\text{gender}} \text{Gender}_i + \beta_{\text{hit}} \text{Hit}_i \end{aligned}$$

The posterior distribution appeared consistent with a multivariate Gaussian. All parameters except gender (-.386[-.955, .0161]) uniquely predicted variance in mathematics attainment, with: year group (1.13[.797, 1.38]); and proportion hit (.666[.356, .975]).

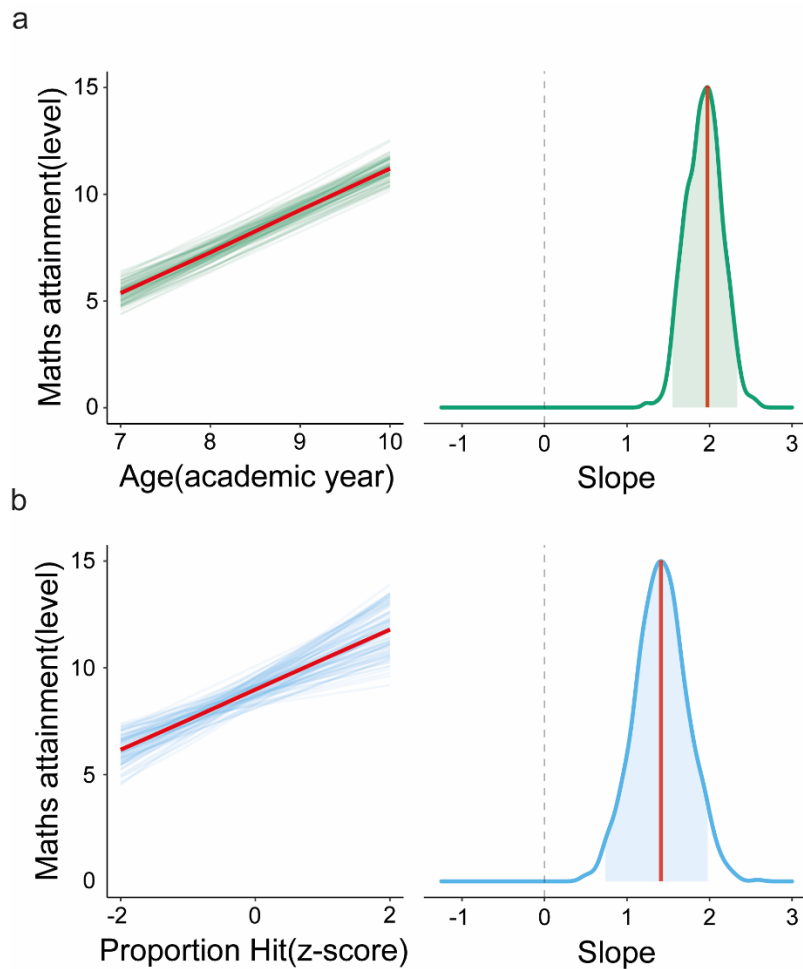


Figure 2.2. Marginal posterior distribution of the mathematics attainment model in adolescents. a) Partialled main effect of age. b) Partialled main effect of proportion of targets hit. Left: fine lines represent a single sample (100 shown for each estimate) of the posterior distribution, with the bold red line the MAP estimate. Right: the corresponding distribution of slope values. The red vertical line represents the MAP estimate, the shaded area under the curve is the 95% HDPI.

Our estimates of outcome levels from 1000 samples of the posterior distribution can be interpreted as if they were coefficients from a linear model (46). The MAP estimate shows that each yearly increase in academic year corresponds to an improvement of 1.97(1.55, 2.34) levels in mathematics per year (Fig. 2.2a). For comparison, MAP estimates of the partial effect of the proportion of targets hit show an associated increase in mathematics attainment of 1.41(.737, 1.98) levels (Fig. 2.2b) per SD.

Therefore, each SD increase in task performance corresponds to ~7 months' improvement in mathematics attainment

2.4. The Role of Executive Control

Having replicated the link between interceptive timing and mathematics in an adolescent population, we combined adolescent data with the data previously collected from school children (19). Firstly, we wanted to see whether the magnitude of the relationship was age invariant, a larger association in school children would imply a larger role for executive functions as executive functions play a greater role in sensorimotor performance at younger ages (43). Second, we controlled for inhibitory control directly in our models by including a measure derived from the kinematics. We also considered interceptive timing and inhibitory control as predictors in a model of English attainment to assess whether the independent contribution of sensorimotor ability was domain specific to mathematics.

2.4.1. Derivation of inhibitory control measure (false starts)

Marinovic et al (2009) found participants were able to inhibit interceptive movements if stop signals were presented at least 200ms prior to their initiation, which aligns with the latency to inhibit movements on other stop signal tasks (47). This latency, or the stop-signal reaction time (SSRT), is one of the principal measures of (reactive) inhibitory control and has been linked to academic attainment (48).

Our task did not explicitly introduce a visual stop cue to inhibit prepotent initiation responses, however, visual information was still likely used to interrupt or inhibit premature responses. Approximately 20% of all trials featured movements that were non-mono-phasic (Fig. 2.3). These apparent corrections were made despite very short movement times (~300ms) and the instructions to perform only a single movement when intercepting the target.

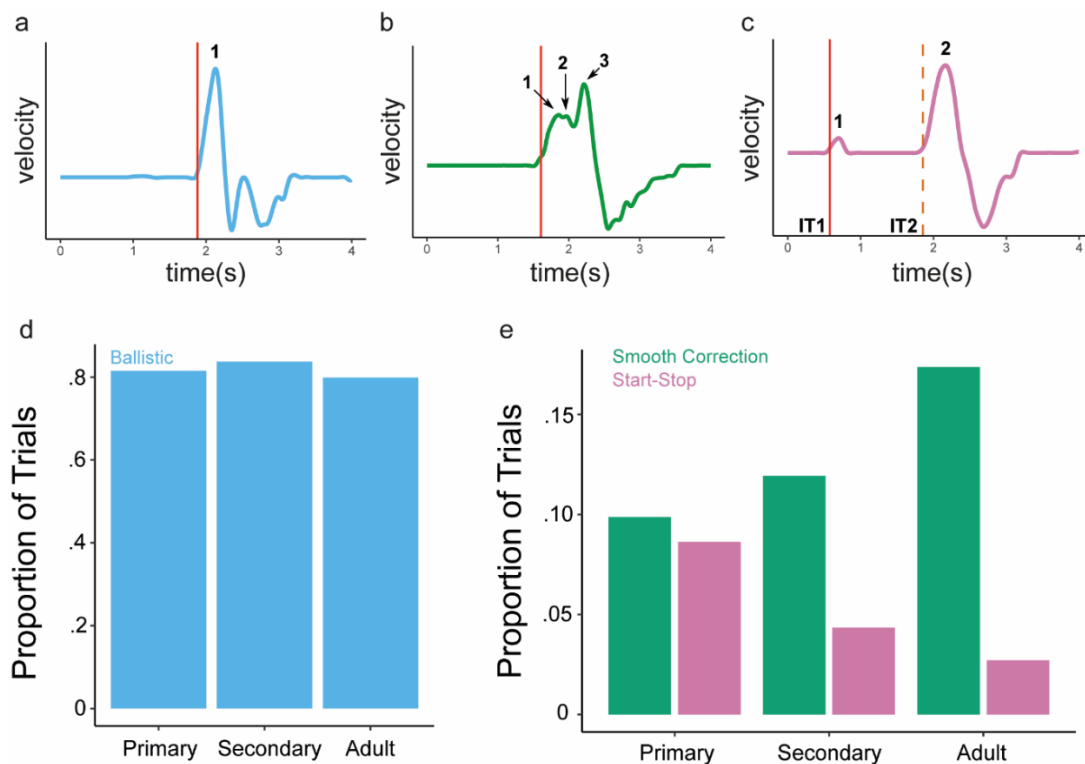


Figure 2.3. Visualising corrected movements. Panels a-c show characteristic velocity-time profiles for different movement types. Numbers correspond to the peaks identified and the red, solid lines represent the initiation time (IT): a) Ballistic movement – a single velocity peak; b) Smoothly corrected movement – multiple peaks whose velocity never dips below the initiation threshold (40mm/s); c) Start-stop movement – multiple peaks with a sub-threshold velocity prior to the interceptive movement. The orange, dotted line represents the IT of the interceptive movement; d-e) The proportion of trials featuring ballistic(blue), smoothly corrected(green), and start-stop(magenta) movements for each cohort (Primary = 5-10 years old; Secondary = 11-15; Adult = 18+).

Assuming participants were able to use visual information to *interrupt* prepotent initiation on trials where corrections were observed, we expected the same information was used to *inhibit* movements on trials where false starts were not observed (32). Given this information must be available 200ms prior to initiation (32, 47), a measure of inhibitory control can be constructed. Any movement initiated 200ms prior to our estimate of when participants would correctly initiate their movement is taken to represent a failure to inhibit a prepotent initiation in response to the visual information available, or a “trigger failure” of the stop signal (49). We employ the proportion of trials on which these *false starts* occur as our measure of inhibitory control.

Estimates of expected initiation times have previously been made by training participants to hit targets at a fixed movement time and finding the mean initiation time (32, 50-51). In our task, movement times were completely unconstrained. If participants were performing the task correctly, it is common to observe reduced movement times in response to faster, narrower targets (52-53). Ideally, therefore, separate initiation times should be calculated for each combination of target speed and width per participant. With just six trials per combination of speed and width, and a variable amount of hits and ballistic movements, it was impossible to make reasonable estimates. Accordingly, we grouped trials by speed only, yielding a maximum of 18 trials per estimate. Speed was chosen, rather than width, because speed is the more salient visual cue when reducing movement times (54) and represented a proportionally greater reduction of the timing window per level in our conditions. Participants with fewer than three

successful hits using ballistic movements at any given speed were excluded from this analysis, (N= 20).

2.4.2. Attainment scores

In the primary school cohort, current attainment scores in mathematics, reading, and writing, were assigned by class teachers on a curriculum-aligned, standardized linear scale (range 1-15). The standardized attainment scales for primary and secondary schools differ, so they were aligned using government grades linking KS2 assessments to GCSE attainment levels (Supplement C). The resulting scale ran from 1-34, with linear progression through academic years 1-10 (Supplement C). To compare English assessments between cohorts, the mean of reading and writing was taken as the overall English attainment score for the primary school.

As above, participant age was grouped by academic year rather than chronological age, centered around the median year group. For years 1-10, our centered age ranged from -4.5 to 4.5, with single unit increments.

2.4.3. Measure validation

We constructed two models to confirm the suitability of our interceptive timing measure. The first predicted the proportion of targets hit to confirm that performance increases between the three cohorts were approximately linear and there were no floor or ceiling effects (Supplement A). The second predicted movement time from target speed and width to confirm participants of all ages acted optimally by making briefer movements for targets with greater timing demands (Supplement A).

To confirm the suitability of our inhibitory control measure, we constructed a model predicting the incidence of *false starts* based on age, target speed, whether the trial was preceded by a faster target, and whether the trial was presented earlier or later in the experimental session. This was to confirm the incidence of *false starts* declined with age, correlated with the prepotent response to act earlier based on trials immediately prior, and was not a feature of initial task exploration (Supplement B).

2.4.4. Academic attainment

The proportion of targets hit and the proportion of false starts were standardized as z-scores (mean = 0, sd =1) so that parameters were directly comparable. As above, there were five students who attained a higher attainment score than 22 in mathematics (scores: 25, 26, 28, 28, 31). To ensure levels were not underpopulated, they were grouped into the nearest rounded mean level (score = 28). A saturated ordinal logistic regression model was constructed to predict mathematics attainment from all plausible combinations of predictors, including all combinations of interactions with year group:

$$Mathematics_i \sim Ordered(p)$$

$$\begin{aligned} \text{logit}(p_k) = & \alpha_k + \beta_{year}Year_i + \beta_{gender}Gender_i + \beta_{hit}Hit_i + \\ & \beta_{fs}FalseStart_i + \beta_{year}\beta_{hit}Year_iHit_i + \beta_{year}\beta_{fs}Year_iFalseStart_i + \\ & \beta_{year}\beta_{hit}\beta_{fs}Year_iHit_iFalseStart_i \end{aligned}$$

The parameters were fit using the same specification as above, with additional models fit in which parameters were systematically eliminated. The final model, a null model, contained only intercepts for each

level of outcome. As above, the best model was selected by applying the Leave One Out Information Criterion (LOOIC) and comparing weights (44).

The posterior distribution of the best performing model was inspected as above. Likewise, outcome levels were estimated from 1000 samples of the posterior distribution to transform parameters to a more intuitive scale. The same procedure was repeated using English attainment as the ordinal outcome. There was one participant with an English attainment score of 22, they were placed at 21 to avoid underpopulated levels.

2.4.5. Results

2.4.5.1. Measure validation

First, we assessed the suitability of our interceptive timing measure. Our models of the proportion of targets hit and movement time show that mean performance improved linearly with age, with a wide range of performance across groups (Fig. 2.4), and that all ages behaved optimally by making briefer movements in response to greater timing constraints (Fig. 2.5). See Supplement A for further details.

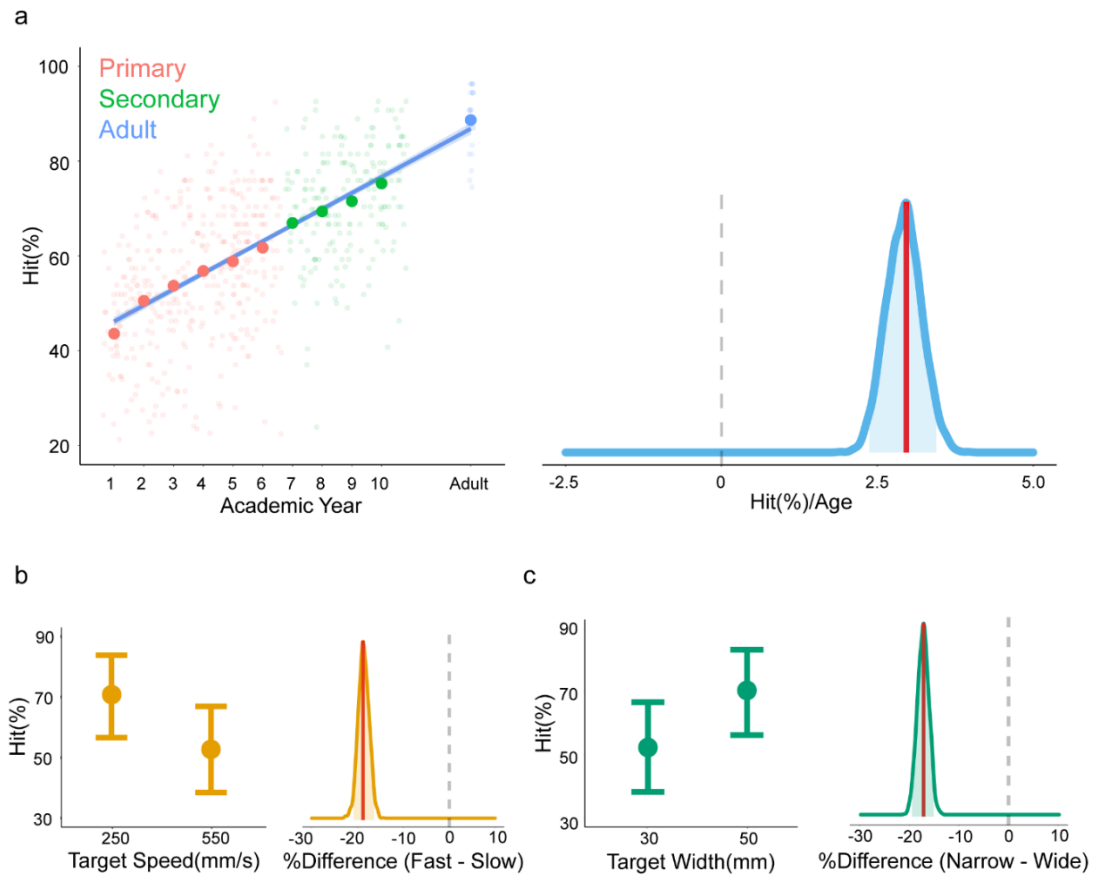


Figure 2.4. Model of interceptive timing performance. a) The effects of age. Left: Performance increases with age. Large dots represent observed mean year group performance; small dots represent individuals. Dots are coloured according to cohort; red, primary school; green, secondary school; blue, adult. Adults are placed at year 13 (i.e. the academic year which would include 18 year olds). The thick blue line represents MAP value of posterior distribution at each level of academic year, with light blue shadow representing 95% HDPI. Right: Posterior distribution of parameter estimate for academic year. Each year corresponds to ~3% improvement. The red line represents MAP value, shading under curve is the 95% HDPI. b) Fewer fastest targets were hit. Left: Posterior distribution of intercepts for the slowest and fastest targets. Large dot represents MAP value with error bars at 95% HDPI. Right: Posterior distribution of performance difference between fastest and slowest targets. c) Fewer narrowest targets were hit. Left: Posterior distribution of intercepts for the widest and narrowest targets. Large dot represents MAP value with error bars at 95% HDPI. Right: Posterior distribution of performance difference between narrowest and widest targets.

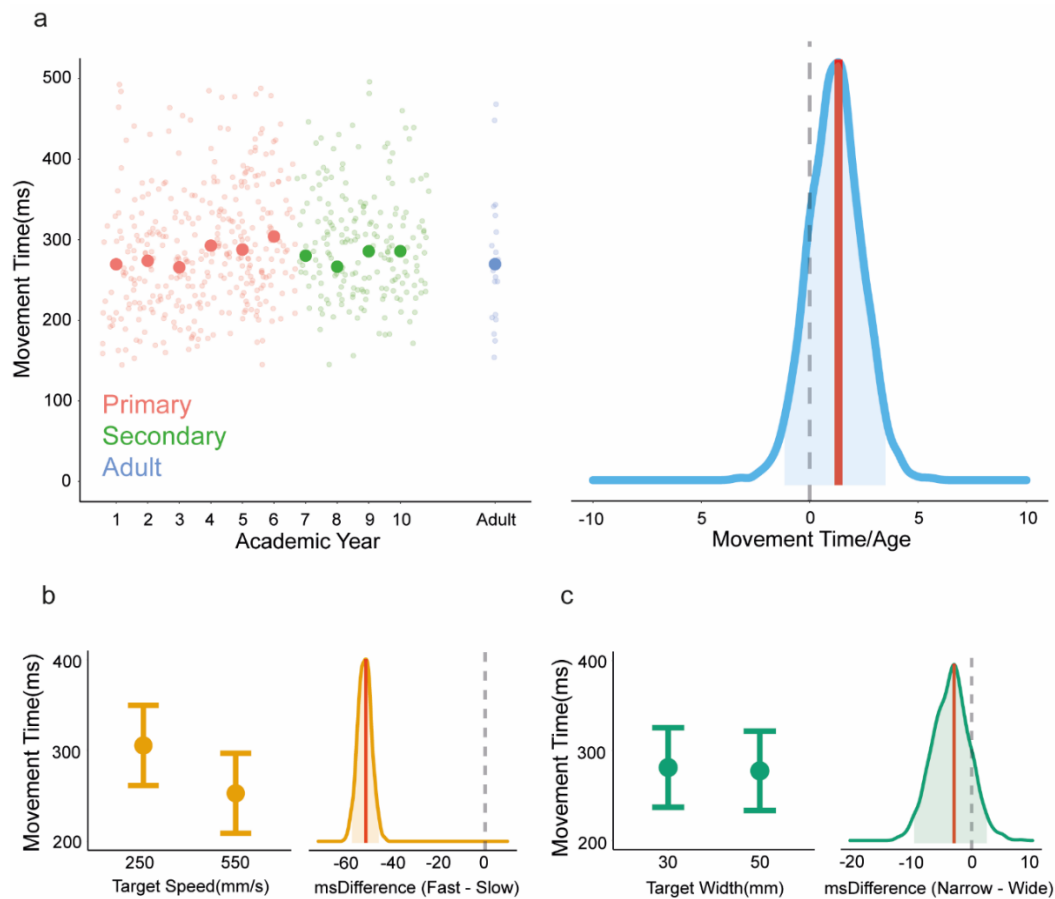


Figure 2.5. Model of movement time. a) The effects of age. Left: Movement time is not affected by age. Large dots represent observed mean year group performance; small dots represent individuals. Dots are colored according to cohort; red, primary school; green, secondary school; blue, adult. Adults are placed at year 13 (i.e. the academic year which would include 18 year olds). Right: Posterior distribution of parameter estimate for academic year. HDPI interval is zero spanning. Red line represents MAP value, shading under curve is the 95% HDPI. b) Briefer movements were made at faster target speeds. Left: Posterior distribution of intercepts for the slowest and fastest targets. Large dot represents MAP value with error bars at 95% HDPI. Right: Posterior distribution of movement time difference between fastest and slowest targets. c) There was no change in movement time for different widths. Left: Posterior distribution of intercepts for the widest and narrowest targets. Large dot represents MAP value with error bars at 95% HDPI. Right: Posterior distribution of movement time difference between narrowest and widest targets.

Second, we assessed the suitability of our inhibitory control measure.

Our model shows participants made fewer false starts as they got older, made more false starts on targets that were preceded by a faster target, and did not make more false starts on earlier trials (Fig. 2.6). See Supplement B for further details. Confident that our measures of interceptive timing and

inhibitory control were suitable, we considered them as predictors in models of attainment to partial out their effects.

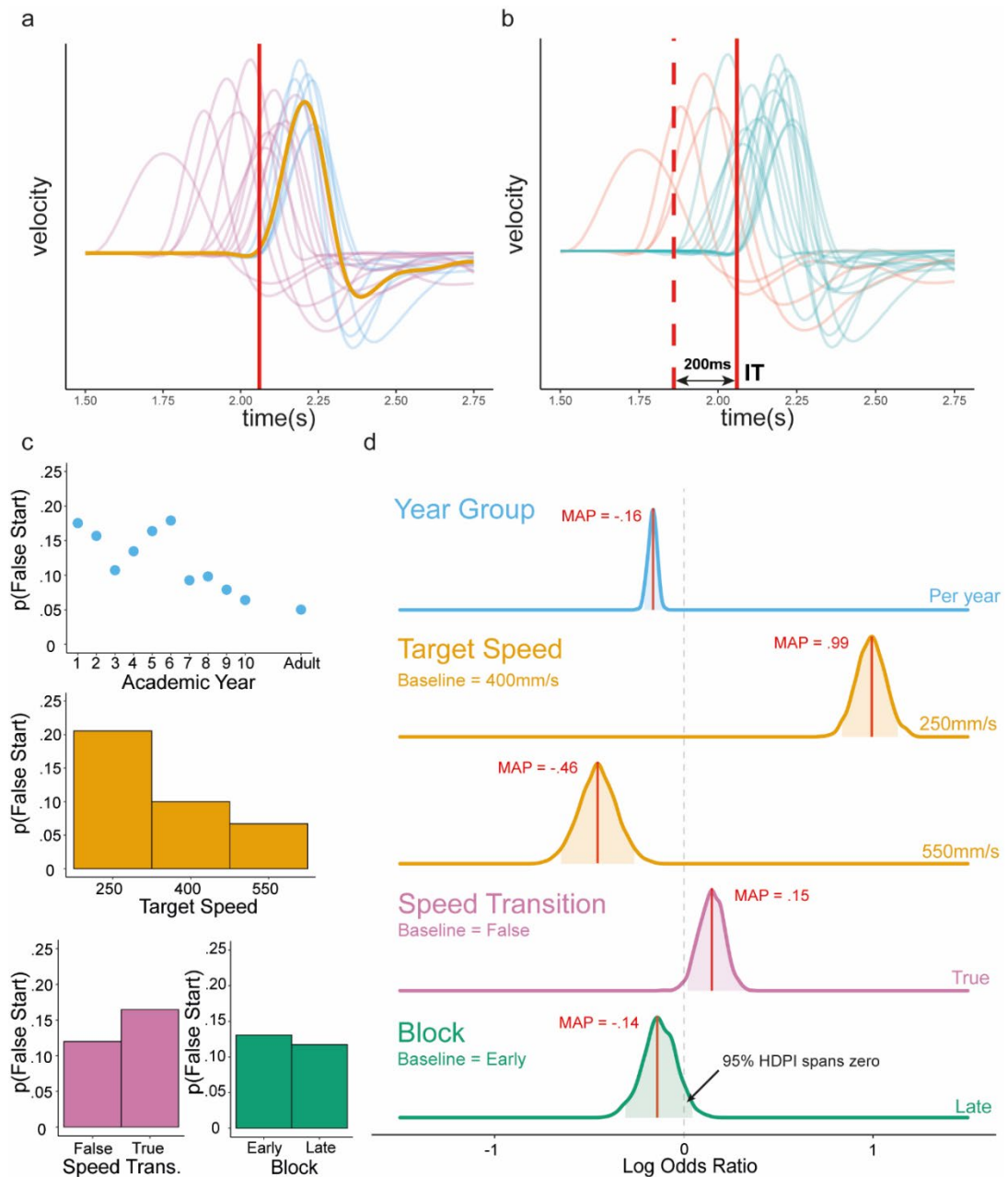


Figure 2.6. Classifying and modelling false start movements. Top: Each trace represents all trials at one of the three target speeds (i.e. 18 total). Both plots are from the same participant at the same speed. a) Calculating the mean initiation time (IT). Blue traces are ballistic movements on which a hit was recorded. Magenta traces are those that were non-ballistic and/or missed. The orange trace shows the mean aggregate solution from which the IT was derived. b) False starts. The dotted line shows the 200ms threshold prior to initiation before which participants can inhibit their movements. Thus the red traces are those that are classified as false starts (inhibitory “trigger failures”). Bottom: Observed and modelled false starts. c) The total proportion of early movements at each level of age, target speed, speed transition, and block of the experiment. d) Parameter estimates from our model of

false starts for age (reference level: secondary school), target speed (reference level: 400mm/s), speed transition (reference level: false) and block of the experiment (reference level: early). The central red line represents the MAP, with the shaded area containing the 95% HDPI.

2.4.6. Academic attainment

We combined our *de novo* adolescent interceptive timing data (ages 11-15) with previous data from a primary school (ages 5-11) and considered a kinematic measure of inhibitory control in models of mathematics and English attainment. We found both the number of targets hit, and the number of false starts predicted mathematics attainment independently of age, gender, and each another. Considering all combinations of predictors in models for mathematics, the best performing model contained year group, gender, proportion of targets hit, and proportion of false starts as predictors, with no interaction effects:

$$\begin{aligned} \text{Mathematics}_i &\sim \text{Ordered}(p) \\ \text{logit}(p_k) &= \alpha_k + \beta_{\text{year}} \text{Year}_i + \beta_{\text{gender}} \text{Gender}_i + \beta_{\text{hit}} \text{Hit}_i + \\ &\beta_{\text{fs}} \text{FalseStart}_i \end{aligned}$$

The posterior distribution appeared consistent with a multivariate Gaussian. All parameters except gender (-.344[-.692, .017]) uniquely predict variance in mathematics attainment, with: year group (1.38[1.25, 1.52]); proportion hit (1.32[.993, 1.68]); and proportion of false starts (-.188[-.361, -.009]).

Considering estimates from 1000 samples of the posterior distribution, the MAP values show that for every 1SD increase in the proportion of false starts, there is an associated change in mathematics

attainment of $-.259(-.471, -.032)$ levels. Conversely, for every 1SD increase in the proportion of targets hit, there was an associated increase in mathematics attainment of $.787(.487, 1.11)$ levels (Fig. 2.7). For comparison, MAP estimates using the partial effect of academic year show an improvement of $1.67(1.58, 1.77)$ levels per year. Therefore, each SD increase in task performance corresponds to ~ 5.5 months' improvement in academic attainment and each SD improvement in inhibitory control corresponds to ~ 2 months' improvement in mathematics attainment.

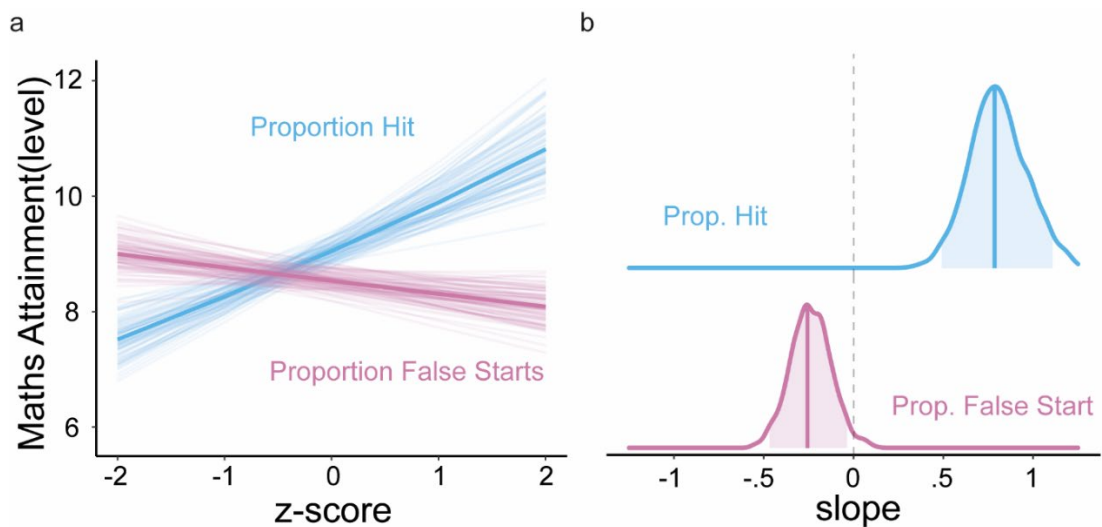


Figure 2.7. Marginal posterior distribution of the mathematics attainment model shows that math attainment is positively associated with task performance and negatively associated with false starts. a) Main effects of proportion of targets hit, and proportion of targets with false starts. Math attainment outcomes were estimated by varying proportion of targets hit (blue) and proportion of false starts (magenta) while holding all other values at their mean. Fine lines represent a single sample (100 shown for each estimate), with the bold line the MAP estimate. b) The distribution of slope values from a. The thick vertical line represents the MAP estimate, the shaded area under the curve the 95% HDPI.

To determine the specificity of the relationship between mathematics attainment and interceptive timing performance, we further considered a model of English attainment. We found that the number of targets hit predicted English attainment independently of age and gender, but

only in participants who made a significant number of false starts. The model that minimized the LOOIC contained parameters for year group, gender, proportion of targets hit, proportion of false starts, and a hit/false start interaction as predictors, there was also a year group/false start interaction, though the 95% HDPI was non-significant (-.114[-.169, .000]):

$$English_i \sim Ordered(p)$$

$$logit(p_k) = \alpha_k + \beta_{year}Year_i + \beta_{gender}Gender_i + \beta_{hit}Hit_i + \beta_{fs}FalseStart_i + \beta_{year\beta_{fs}}Year_iFalseStart_i + \beta_{hit\beta_{fs}}Hit_iFalseStart_i$$

Visual inspection of the posterior distribution revealed a multivariate Gaussian. Year group (1.39[1.26, 1.52]), gender (-1.07[-1.42, -.727]), proportion of targets hit (.360[.129, .583]), proportion of false start movements (-.294[-.486, -.098]), and the hit/false start interaction (.228[.064, .386]) were all significant.

As for the previously reported ordinal logistic regressions, the mean outcome level was estimated from 1000 samples of the posterior distribution. However, because the hit/false start interaction was non-zero, estimates were made at three levels of false start movements (proportion = .0, .1, .2), while varying hit proportion over a range of z-scores (Fig. 2.8).

At zero false starts, the MAP estimate shows that for every 1SD increase in the proportion of targets hit, there is an associated non-significant increase in English attainment of .074(-.238, .452) levels. At a proportion of .10 false starts, there is an associated increase in English attainment of approximately .388(.133, .623) levels per 1SD increase hit performance. Finally, each 1SD increase in hit performance at .20 false starts was associated with an increase of .627(.338, .881) levels. Notably, when no

false start movements are made, the 95% HDPI spans zero (Fig. 2.8), indicating no relationship between hit performance and English attainment. In summary, the relationship between interceptive timing performance and English attainment is mediated by inhibitory control such that those with increasingly poorer inhibitory control have a greater association between their task performance and English attainment. However, there is no relationship between interceptive performance and English between those who do not make false starts.

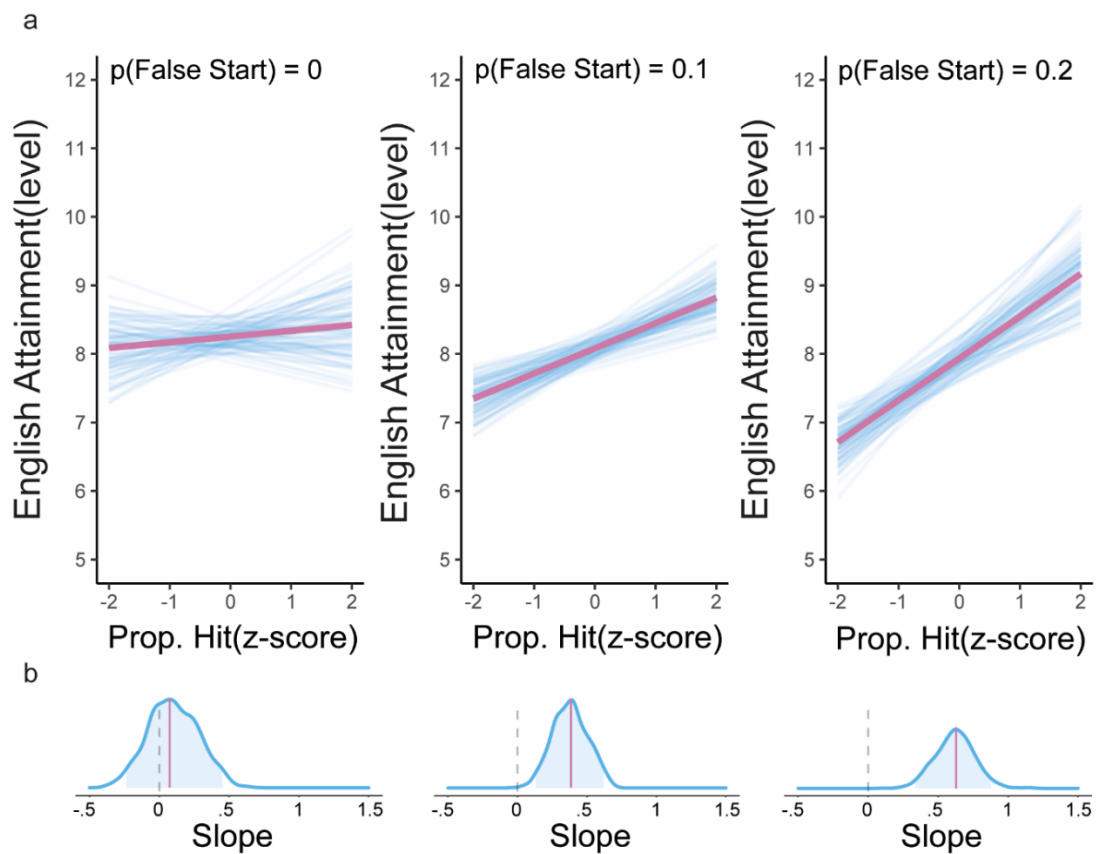


Figure 2.8. Marginal posterior distribution of the English attainment model shows attainment in English is not associated with task performance when no false starts are made. a) Hit/false start interaction. English attainment outcomes were estimated by varying proportion of targets hit at three levels of false starts (left to right: .0, .1, .2) Fine blue lines represent a single sample (100 shown for each estimate), with the bold, magenta line the MAP estimate. b) The distribution of slope values from above. The thick, magenta line represents the MAP estimate, the shaded area under the curve the 95% HDPI. When no false starts are made(top), we do not have

95% certainty there is a non-zero relationship between hitting performance and English attainment

2.5. Discussion

The link between sensorimotor skills, academic attainment and executive function was examined using an interceptive timing task. Replicating our original study with adolescents, we found interceptive timing performance predicted mathematics attainment in this older age group. Combining this with our original data (19) and extracting a kinematic measure of inhibitory control, we found interceptive timing performance uniquely predicted mathematics (and not English) attainment for all levels of inhibitory control, with no age mediated effects.

Previous research has downplayed any functional link between sensorimotor skills and school attainment, because of the confounding effects of executive functions (23, 38-42). The present results, however, suggest executive function does not account for the association between interceptive timing and mathematics. Firstly, the link persisted at all ages (5-15 years old) with no age interactions. If executive functions were overwhelmingly responsible, we would have expected the relationship to diminish in older participants because executive functions have been shown to contribute less to successful motor performance with age (43). Therefore, we suggest the shared variance is accounted for by an alternative, age invariant mechanism. A common neural circuitry between spatiotemporal and numerical operations (5, 8, 11) is a strong possibility because behavioral

links have been shown to persist in children as young as 3 through adulthood (6).

That is not to say executive functions play no role. We have shown that interceptive timing and inhibitory control independently contribute to attainment in mathematics. It is likely previous studies (38-42) failed to find this link because they used the MABC2 (55) to assess sensorimotor skills. The MABC2 is a brief battery of several broadly construed sensorimotor domains, designed to identify movement impairments on a single binary scale (impaired or not), and not as predictors in parametric models. Our task, however, produced a granular measure of a single sensorimotor domain, interceptive timing, with no floor or ceiling effects from 5 years old to adult (Fig. 2.4), eliciting stereotypical differences in movement times (~50ms) in response to increased timing demands (52-53) at all ages (Fig. 2.5).

It is important to emphasize the shared processing hypothesis does not rule out a role for executive control, in fact, it predicts it; some level of external control (inhibitory or otherwise) must operate to generate qualitatively different cognitive processes from common neural substrates. This relationship may be causal in nature, with sensorimotor interactions laying the neural foundation from which mathematical processes later emerge (2-3). Thus, just as the perceptual foundation of mathematics, numerosity, appears to be implicated in temporal representation (18, 22), our findings hint further a functional link between sensorimotor skills that require accurate temporal estimates and later mathematical proficiency.

Our model of English attainment supports this interpretation because the variance it shared with interceptive timing was not independent from our measure of inhibitory control. Rather, interceptive timing ability only predicted English attainment for those individuals that made more false starts (Fig. 2.8). Accordingly, we have some confidence that the variance between mathematics and interceptive timing arises from the specificity of the overlap between mathematical and spatiotemporal processing because independent variance does not exist between interceptive timing and an alternative domain of attainment for which we did not hypothesized neural overlap.

We predicted there would be variance in attainment shared between inhibitory control and interceptive timing if it arose from executive processes necessary to support a shared neural architecture, rather than as a direct consequence of that neural architecture. One possibility is the link between interceptive timing and English attainment may reflect the role of latent attentional processes. Interceptive control shifts towards feedback mechanisms when there is more time to act between initiation and interception (58), which we observed in response to false starts (Fig. 2.3). Therefore, when false starts are made, hitting performance is aided by attentional processes overseeing the ability to make guided corrections (59). Differences in hitting performance in those that make more false starts, therefore, might be accounted for by differences in attention, and this could explain differences in English attainment.

This interpretation is consistent with a broader view of shared processing, in which sensorimotor circuits can be exapted for other abstract processes such as linguistic and semantic representation (2, 4). If

sensorimotor and linguistic processes share the same circuitry, processes implicated in circuit selection, for example, attentional modulation of interneurons (60), are likely to explain variance shared between the two. Moreover, just as the ability to integrate temporal estimates into timed movements independently predicts mathematics attainment, there may be features specific to other sensorimotor skills that could establish an independent link with the acquisition of language. Future work must carefully consider alternative sensorimotor measures to confirm the domain specificity of relationships with attainment that are independent from executive control.

Of course, our interpretation must be met with a degree of further caution, and a longitudinal study is required to confirm causal mechanisms. Indeed, the extent to which early sensorimotor interactions define later attainment remains unclear, and though shared processing suggests interceptive timing is a *contributory cause* towards mathematics attainment, the causal relationship extends only as far as any functional overlap between the neural substrates for the respective tasks. To be clear, there are a multitude of processes in each domain unlikely to be meaningfully linked, and we do not suggest improvement in interceptive timing necessarily yields in-kind improvements in mathematics (or vice-versa). Indeed if, in a Piagetian sense, abstract processes emerge from sensorimotor interactions in infancy, it is likely too late for improvements in interceptive timing to yield like-for-like improvements in mathematics. Ultimately, the practical implications of this research are likely to be limited to the more precise identification of barriers to children's mathematical development. For

example, helping to distinguish between executive or representational deficiencies.

Additionally, without better measures of executive control, we cannot discount the possibility that any independent relationship is a consequence of the executive processes involved in task execution being distinct from those responsible for stopping task execution. While our kinematic measure of inhibitory control successfully met several empirical assumptions, overall incidence of false starts was low (Fig 2.6), and stop-signal reaction time, estimated from participants inhibiting movements in response to stop cues, is the gold standard measure of reactive inhibition (56). Furthermore, it has been suggested proactive inhibition (i.e., the tendency to delay response under the uncertainty of whether a stop cue is going to be presented) may be the more relevant sub-domain when considering naturalistic behaviors and atypical development (30). Similarly, we did not take measures of updating and shifting. And while inhibitory control is likely a fair marker of executive function overall - inhibition is highly correlated with updating and shifting, perhaps even indistinguishable (25, 57) - additional measures may share further variance. Finally, therefore, reactive and proactive measures of inhibition, and measures of updating and shifting, are needed if we are to demonstrate unambiguously a direct link between interceptive timing and mathematics attainment.

In conclusion, combining adolescent and primary school data and considering trials on which false starts were made, we found while the relationship between interceptive timing and English attainment was mediated by inhibitory control, the relationship with mathematics was not.

This supports a shared processing view in which a common neural architecture is implicated in both sensorimotor and more abstract domains of cognition. More specifically, it is consistent with the idea sensorimotor circuits are exapted for later emerging mathematical processes. Nevertheless, further research is required to unambiguously characterize this as a domain specific, causal relationship that emerges as a direct consequence of shared processing, rather than from the executive processes necessary to support shared processing. In the absence of longitudinal studies deploying adequate sensorimotor measures that account for domain specific associations in attainment in terms of executive functions, we maintain there is a distinct functional link that cannot be explained in terms of general processes.

Disclosures

We are not aware of any conflict of interest, financial or otherwise, regarding the subject matter and materials discussed in this article, for any of the authors, or their academic institutions or employers.

Endnotes

Supplementary materials including source code for the task, anonymised data for both experiments, along with the data analysis scripts and visualisations are available in an online repository at <https://osf.io/yq2r5/>

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2.7. Supplementary Materials

2.7.1. Supplement A: Interceptive timing measure validation

To assess the suitability of our interceptive timing task, we considered a couple of linear mixed effects models. Firstly, we considered whether participants were performing as expected over the range of difficulties. We expected fewer of the fastest, narrowest targets (i.e. those with the smallest timing window) to be hit relative to the slowest, widest targets. In addition, we expected the number of targets hit to improve with age and, as a suitable parametric measure, without observing floor or ceiling effects. Accordingly, our first model predicted the proportion of targets hit from target speed, target width, and year group. In this case, adults were assigned to year 13 (i.e. the first academic year to include 18 year olds), with year group centered around the median (year 7). All interaction terms were included, and random intercepts estimated for each participant to control for within participant variability.

Parameters were estimated by Bayesian estimation, using a No-U-Turn Sample algorithm as implemented in the *brms*(ver. 2.9.0) package for R (ver. 3.6.0), with 2 chains performing 1000 warmups followed by 2000 iterations (Kurz, 2018). To ensure our estimates were conservative, all parameters were assigned weakly informative priors (fixed effects: Normal[0, 1]; random effects: Cauchy[0, 1]). Chains were visually examined to ensure they converged. The posterior distribution was then inspected. Parameters with a non-zero spanning 95% highest density posterior interval (HDPI) were considered significant. For significant parameters, the *maximum*

a posteriori (MAP) value was taken as a point estimate of the mean difference in performance with respect to reference values.

Secondly, we considered if participants moved with shorter movement times (i.e. more quickly) towards the fastest, narrowest targets, relative to the slowest and widest. This has been observed in prior studies and is thought to be the optimal strategy to reduce error (e.g. Tresillian and Houseman, 2005). Accordingly, the second model predicted participants' movement times. It was identical to the first in all respects except the fixed effect priors were normally distributed with a mean of 50 and a standard deviation of 25 to conservatively account for the difference in scale of the dependent variable.

Considering the first model, from the maximum a posteriori (MAP) values and the 95% highest density posterior intervals (HDPI) of the percentage of targets hit, the parameters for academic year (2.96[2.36, 3.45]), target speed (-18.8[-20.1, -16.2]), and target width (-17.2[-19.6, -14.8]) were non-zero spanning, denoting differences with 95% certainty (Figure 2.4). Specifically, each academic year corresponds to an average improvement of approximately 3%, with the youngest participants in year 1 estimated to hit 43.5%[41.4, 45.6] of targets on average, and the adult cohort estimated to hit 84.1%[82.0, 85.0]. Moreover, participants hit more of the slowest targets (70.8[56.6, 83.5]) than the fastest (52.7[38.4, 67.0]), and more of the widest targets (70.1[55.9, 83.1]) than the narrowest (53.5[39.2, 67.7]).

Our model of movement time (Figure 2.5) shows that of the parameters for academic year (1.18[-1.17, 3.58]), target speed (-54.2[-60.3, -48.1]), and target width (-3.35[-9.40, 2.65]), only target speed had a non-zero spanning 95% HDPI. Accordingly, participants of all ages made briefer movements towards the fastest targets (253ms[209, 297]) compared to the slowest (306ms[261, 350]).

Thus, the validity of our interceptive timing measure was confirmed from canonical observations that in response to greater timing demands (i.e. faster targets), participants made briefer movements to reduce error (Tresillian 2005; Tresillian and Lonergan, 2002; Tresillian et al., 2004), which was true at all ages (Figure 2.5). While we did not observe briefer movements in response to narrower targets, the levels of speed we tested had a disproportionately greater influence on the timing window (speed $250/550 = 0.45$) than the levels of width ($30/50 = 0.6$), further compounded by the fact target speed is a more salient visual cue than width at reducing movement time (Tresillian, Oliver, and Carroll, 2003).

2.7.2. Supplement B: Inhibitory control measure validation

While inappropriate prepotent response counts have previously been used as a measure of inhibitory control (e.g. Donati et al., 2012; St Clair-Thompson and Gathercole, 2006), because explicit stop cues were not presented in our task, there are a number of additional concerns to address directly. Firstly, we would expect a reduction in false starts as participants age as inhibitory control improves through childhood and adolescence (Williams et al., 1999). Secondly, if false starts are prepotent responses built

up from expectations set by previous trials (de Lussanet, smeets, and Brenner, 2002), we would expect a greater incidence of false starts on trials where there is a transition in speed from faster to slower targets. Thirdly, there is the concern that movement variability is at its greatest when participants begin learning a task (Dhawale, Smith, and Olveczky, 2017). Through a process of trial and error, task space exploration steers the sensorimotor system towards patterns of behaviour that improve performance over time (Shadmehr, Huang, and Ahmed, 2016). Conversely, the ability to successfully inhibit prepotent responses is relatively fixed, with little trial-by-trial variability when there are fewer than 120-150 trials (Matzke, Verbruggen, and Logan, 2020). Therefore, if there is no difference in the incidence of false starts on earlier trials, relative to later trials, we can discount the possibility our measure is capturing initial task space exploration. To address these concerns, trials were coded by two additional factors. Firstly, *speed transition* denoted whether the trial was preceded by a trial with a faster target speed. Secondly, each speed was separated into two experimental stages, with the first three blocks at each speed assigned as *early*, and the second three blocks assigned as *late*. The order of trials and how they were coded is contained in table 2.S1.

Table 2.S1. Experimental blocks. Each block consisted of 3 trials (54 total) with one of 9 combinations of target speed and target width, each combination appearing twice. Blocks were binned according to target speed by their order of appearance, with the first three blocks at that speed classified as EARLY, and the latter three blocks as LATE. Blocks were additionally coded based on whether they proceeded a block of faster targets.

Block	Target (mm/s)	speed	Target (mm)-	width	Early/Late	Speed Trans
1	250		40		EARLY	FALSE
2	250		30		EARLY	FALSE
3	250		40		EARLY	FALSE
4	400		30		EARLY	FALSE
5	400		40		EARLY	FALSE
6	400		50		EARLY	FALSE
7	400		30		LATE	FALSE
8	550		30		EARLY	FALSE
9	400		40		LATE	TRUE
10	250		50		LATE	TRUE
11	550		50		EARLY	FALSE
12	400		50		LATE	TRUE
13	550		40		EARLY	FALSE
14	250		30		LATE	TRUE
15	550		50		LATE	FALSE
16	550		30		LATE	FALSE
17	550		40		LATE	FALSE
18	250		50		LATE	TRUE

A mixed effect binomial logistic regression was constructed to predict the incidence of false starts for each participant given: their year group (centered around 7), target speed (250, 400[reference], 550); speed transition(*true*, *false*[reference]); and block(*early*[reference], *late*); and all combinations of interactions. Random intercepts were estimated for each participant to control for within participant variability. Reference levels for speed were taken at the median level because we can account for differences at all levels without running multiple comparisons, assuming the effects are monotonic.

Parameters were estimated by Bayesian estimation, as above using weakly informative priors (fixed effects: Normal[0, 1]; random effects: Cauchy[0, 1]). For significant parameters, the MAP was taken as a point estimate of the log odds of a false start being made in performance with respect to an increment of 1 year (year group) or reference values (all other parameters). The odds ratios were calculated by finding the exponent of the MAP and 95% HDPI for each parameter.

Using our model, we were able to quantify the relationship between false starts and each predictor, ascertaining their significance (Figure. 2.6d). We calculated odds ratios by finding the exponent of each parameter to offer a more intuitive translation of our regression parameters. For example, our MAP estimate indicates that for each successive academic year, participants are .850 times likely (i.e. 1.18 times *less* likely) to make a false start, with 95% of estimates ranging between .810 (1.23 times less likely) and .887 (1.13). Furthermore, participants were 2.70(2.26, 3.10) times more likely to make an early movement on the slowest target trials (250mm/s), and .634(.520, .773) times as likely (1.58[1.92, 1.29] times *less* likely) on the fastest target trials (550mm/s), compared to baseline (400mm/s). Our estimate of the effect of speed transition indicates participants were 1.16(1.05, 1.31) times as likely to make a false start on trials proceeding a faster target speed. Nevertheless, our estimate for early versus late trials (.869[.732, 1.02]) reveals that participants are no more or less likely to make false start movements in *early* or *late* trials with 95% confidence. In summary, false start movements were less likely to be made as participants got older, at the slowest target speeds, if the trial followed a

faster target speed, and these effects acted independently of one another. There was no effect, however, of how early the trial was presented.

Thus the validity of our inhibitory control measure was confirmed empirically. Firstly, a greater number of false starts were made on trials that were preceded by faster targets. This is consistent with an interpretation of false starts as inhibition control failures of prepotent responses that are conditioned by exposure to previous trials that strongly influence timing characteristics (de Lussanet, Smeets, and Brenner, 2002). Secondly, there was no difference in the proportion of movements classified as false starts on trials that appeared in the earlier blocks at each speed. Therefore, the measure is not a reflection of learning via exploration of initiation times (Dhawale, Smith, Checzky, 2017; Shadmehr, Huang, and Ahmed, 2016). In addition, there was an improvement in inhibitory control as participants aged (Figure 2.6; Smittenaar et al., 2015; Williams, Ponesse, and Schachar et al., 1999).

Finally, it was important to confirm that trials identified as false starts did not simply contain a subset of missed trials. In this case, the parameters for the proportion of targets hit and false starts would be highly correlated. Pairwise plots from the posterior distribution of our best performing models revealed a multivariate gaussian distribution (Figure 2.S1a-b). Therefore, we are confident parameters for the proportion of targets hit and the proportion of false starts do not mask one another's relationship with attainment.

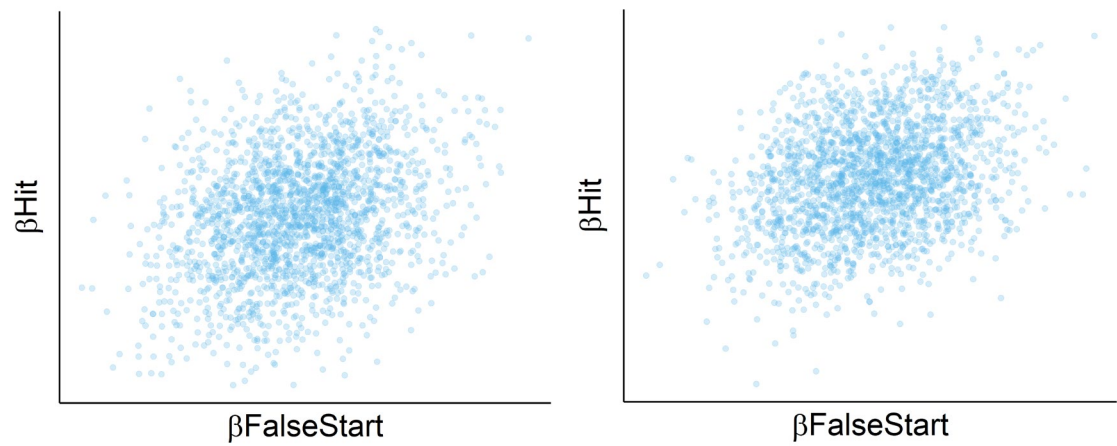


Figure 2.S1. Pairwise plots of False Start and Hit parameters drawn from the posterior distribution of our best performing mathematics (left) and English (right) models. Parameters are distributed normally with no correlations.

2.7.3. Supplement C: School Attainment Metrics

Table 2.S2. Attainment score conversion table. A scale of 1 to K (where K was the highest observed score in the data) was used for the Bayesian Attainment Model. This scale maps to the UK nationally standardized scores. The school year and age at which children are expected to achieve these scores is shown.

Attainment Score	Government Code	Primary standardized score	GCSE level	Secondary standardized score	Expected year group(age)
1	1c	1			
2	1b	2			
3	1a	3			
4	2c	4			
5	2b	5			2(5-6)
6	2a	6			
7	3c	7			
8	3b	8	1	1	
9	3a	9		2	
10	4c	10		3	

11	4b	11	2	4	6(10-11)
12	4a	12		5	
13	5c	13		6	
14	5b	14	3	7	9(13-14)
15	5a	15		8	
16	6c			9	
17	6b		4	10	10(14-15)
18	6a			11	
19	7c			12	
20	7b		5	13	11(15-16)
21	7a			14	
22	8c			15	
23	8b		6	16	
24	8a			17	
25				18	
26		A	7	19	
27				20	
28				21	
29		A*	8	22	
30				23	
31				24	
32			9	25	
33				26	
34				27	

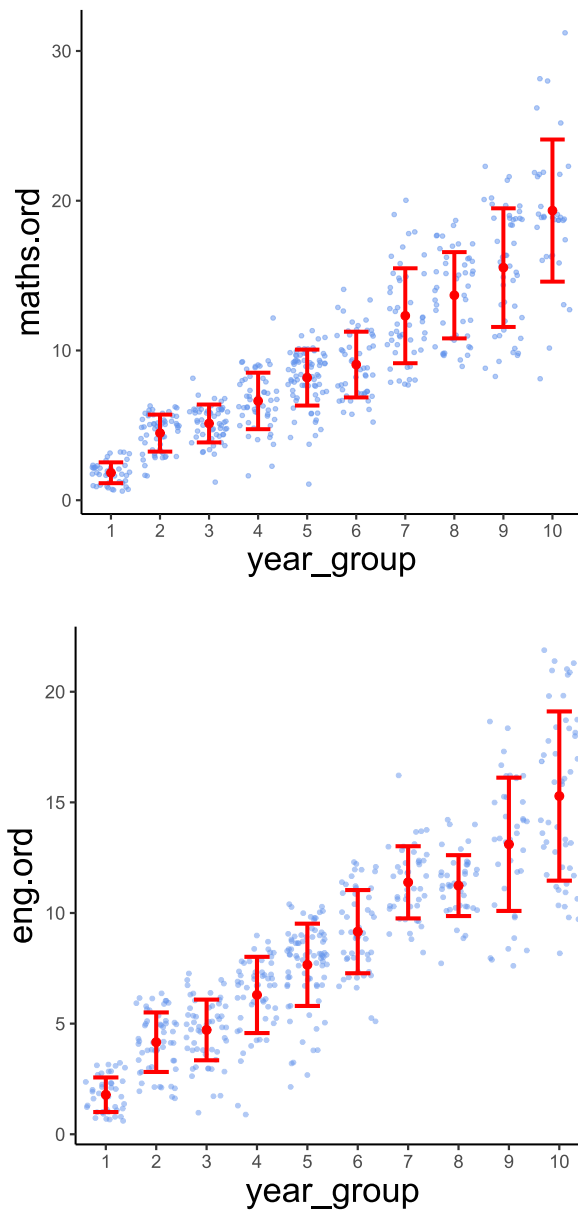


Figure 2.S2. Attainment scores derived from standardized scores provided by primary and secondary schools. Blue dots represent individuals, red dots year group means, and error bars year group standard deviations.

2.7.4. Supplement D: BRMS model specification

Code snippets from the saturated and best performing models are included below for those familiar with the brms package looking for an intuitive specification. The complete dataset and full scripts can be found in the OSF repository (<https://osf.io/yq2r5/>).

2.7.4.1. Adolescent models of mathematics attainment

```
saturated_model <-
  brm(adolescent_data, family = cumulative,
    formula = maths.ord ~ 1 + year_group.c + gender +
hit.z +      year_group.c:hit.z,
    prior = c(prior(normal(0, 1), class = Intercept),
              prior(normal(0, 1), class = b))....

best_model <-
  brm(adolescent_data, family = cumulative,
    formula = maths.ord ~ 1 + year_group.c + gender +
hit.z,      year_group.c:hit.z,
    prior = c(prior(normal(0, 1), class = Intercept),
              prior(normal(0, 1), class = b))....
```

2.7.4.2. Combined models of mathematics attainment

```
saturated_model <-
  brm(combined_data, family = cumulative,
    formula = maths.ord ~ 1 + year_group.c + gender +
hit.z +      early.z + year_group.c:hit.z +
              year_group.c:early.z +
early.z:hit.z +
  year_group.c:early.z:hit.z,
    prior = c(prior(normal(0, 1), class = Intercept),
              prior(normal(0, 1), class = b))....

best_model <-
  brm(combined_data, family = cumulative,
    formula = maths.ord ~ 1 + year_group.c + gender +
hit.z +      early.z
    prior = c(prior(normal(0, 1), class = Intercept),
              prior(normal(0, 1), class = b))....
```

2.7.4.3. Combined models of English attainment

```

saturated_model <-
  brm(combined_data, family = cumulative,
      formula = eng.ord ~ 1 + year_group.c + gender +
hit.z +          early.z + year_group.c:hit.z +
                  year_group.c:early.z +
early.z:hit.z +
  year_group.c:early.z:hit.z,
      prior = c(prior(normal(0, 1), class = Intercept),
                prior(normal(0, 1), class = b))....

best_model <-
  brm(combined_data, family = cumulative,
      formula = eng.ord ~ 1 + year_group.c + gender +
hit.z +          early.z + year_group.c:early.z +
early.z:hit.z
      prior = c(prior(normal(0, 1), class = Intercept),
                prior(normal(0, 1), class = b))...

```

2.7.5. References

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Chapter 3: Proactive inhibition of interceptive actions involves explicit changes to movement planning

From surgery to sport, the ability to countermand an unfolding action is an essential component of skilled behaviour. Inhibition is thought to be implemented through distinct reactive or proactive mechanisms. Reactive control is a well-characterised phenomenon where movement is rapidly stopped in the final stages of its initiation. Nevertheless, our understanding of the mechanisms underpinning proactive inhibition is limited and based entirely on tasks involving button presses. We created a novel, ecologically valid, interception task that allowed rich quantification of proactive inhibition. We also developed a technique to measure participants' explicit awareness of their adopted strategy. We found participants delayed movement onset, increased movement speed, and changed where on the target they hit when there was a chance a stop-signal could be introduced. Importantly, participants were aware of both their delayed onset and change in aim. These findings suggest that proactive inhibition can operate as a compensatory strategy downstream of movement onset. Moreover, we found this is largely, but not entirely, governed by explicitly retrievable strategies. These results challenge current theories of inhibition and show that proactive mechanisms should not be simply characterised as either response delay or response suppression.

3.1. Introduction

In baseball, batters must not only plan and execute an accurately timed swing, but also inhibit movement in response to an errant pitch. Successful inhibition can be implemented reactively, driven by a stop-signal (Logan & Cowan, 1984) (e.g., the pitch veering off course), or proactively, by preparing to stop in anticipation of a stop-signal (Aron, 2011). Reactive inhibition has been explored in a range of contexts, including simple reaction times (Li, Huang, Constable, & Sinha, 2006; Logan & Cowan, 1984), choice reaction times (Rae et al., 2018; Senderecka, Grabowska, Szewczyk, Gerc, & Chmylak, 2012), anticipation timing (Coxon, Stinear, & Byblow, 2006; Slater-Hammel, 1960; Vink et al., 2005), and interceptive actions (Marinovic, Plooy, & Tresilian, 2009). These studies have shown that people are able to inhibit prepotent movements in response to stop-signals approximately 200ms prior to their initiation. This measure of inhibition, the stop-signal reaction time (SSRT), has been critical to understanding a range of neuropathologies because it is often elevated in conditions characterized by inhibitory deficiencies, such as Parkinson's disease (Bissett et al., 2015), attention deficit/hyperactivity disorder (Dimoska, Johnstone, Barry, & Clarke, 2003; Lijffijt, Kenemans, Verbaten, & Van Engeland, 2005; Van Hulst et al., 2018), addiction (Smith, Mattick, Jamadar, & Iredale, 2014), and obsessive compulsive disorders (Lei et al., 2015).

Movements can be proactively inhibited by delaying their onset, which increases one's chance of detecting a need to stop before initiation (Jahfari et al., 2012; Verbruggen & Logan, 2009; Vink et al., 2005; Vink, Kaldewaij, Zandbelt, Pas, & du Plessis, 2015). In contrast to reactive inhibition, which is

automatic, proactive inhibition is thought to be volitional and strategic (Aron, 2011; Jahanshahi, Obeso, Rothwell, & Obeso, 2015). Accordingly, it has been argued that proactive control may represent the more ecological dimension of inhibition (Aron, 2011). For example, an addict's substance avoidance or the suppression of a child's tics is unlikely to recruit reactive mechanisms in response to external stimuli, but may depend rather on the ability to delay their expression (Aron, 2011). Nevertheless, there is some debate as to how proactive inhibition is implemented. On the one hand, delays to movement onset under stop-signal uncertainty may reflect response suppression (Aron, 2011; Cai, Oldenkamp, & Aron, 2011; Zandbelt, Bloemendaal, Neggers, Kahn, & Vink, 2013), on the other, it may simply reflect delayed facilitation (or a "waiting" strategy) (Rieger & Gauggel, 2002). Our understanding of this phenomenon is limited to simple button press tasks in which response delay is the only signature of proactive inhibition. We hypothesised that the underlying mechanisms of inhibition could be teased apart by considering inhibitory control in the planning and execution of more sophisticated behaviors, such as the swing of a bat.

To examine proactive control, we adapted a task previously used to investigate reactive inhibition in the context of interceptive actions (Marinovic et al., 2009). In this paradigm, the interception point is fixed and the timing characteristics of the movement can be considered in isolation (James R. Tresilian, 2005). Thus, in addition to movement onset (initiation time), this paradigm allows us to investigate the duration of movement (movement time) and the associated end-point error (timing error). Previous interception studies have shown the average timing error remains largely the same over

a range of timing constraints, with any delays in initiation offset by decreases in movement time (J. R. Tresilian & Houseman, 2005; J. R. Tresilian & Lonergan, 2002; J. R. Tresilian, Oliver, & Carroll, 2003). It is thought movement times are programmed in advance based on the required temporal accuracy, and triggered when estimates of the time taken for the target to reach the interception point are equivalent (plus neurophysiological delays) (James R. Tresilian, 2005). According to this scheme, if the triggering of the prepared response is suppressed (i.e., takes longer to complete (Verbruggen & Logan, 2009)), the prepared movement time will be inappropriate to preserve timing error and arrival to the target will be delayed. Alternatively, any delays in facilitation should be offset by a proportional reduction in movement time because it is specified immediately prior to triggering (Marinovic et al., 2009), and can be programmed to reflect this wait.

By comparing the characteristics of timed interceptive movements between conditions in which stop-signals could be presented (Uncertain) and in which they were never presented (Certain), we were able to investigate the mechanisms underlying proactive delays to initiation. We found evidence for both delayed facilitation (shorter movement times) and response suppression (delayed arrival). Notably, these timing characteristics can be expressed spatially, with the position of the target at initiation specifying initiation time and the point of the target hit specifying timing error. This allowed us to quantify the degree to which participants were explicitly aware of their strategies using a spatial assay. We show participants were aware of delays to initiation and arrival, but this does not fully account for the

magnitude of the effects we observed. Collectively, these results challenge classical theories of inhibition and present a new way forward for examining the processes underlying proactive control.

3.2. Results

3.2.1. Task performance met the assumptions of the independent race model of inhibition

We first validated our task, considering whether sensible values of SSRT could be estimated and that behavior was suitably constrained by the presentation of stop-signals. Participants tried to hit a target as it moved “overhead” with a bat controlled by mouse or trackpad (Fig. 3.1A). When the background showed dawn (indicated by the color of the sky), there was a 33% chance a stop-signal (instantly switching to daytime; Fig. 3.1B) could be presented. Participants were asked to withhold their movement in response to the stop-signal (stop-trial) and hit the target in its absence (go-trial). On the subsequent stop-trial, the stop-signal was delayed (cf. brought forward) an additional 50ms if participants successfully inhibited (cf. incorrectly responded).

SSRTs were calculated using the integration method. For this method to yield accurate estimates of SSRT, a number of assumptions must be made. The model states inhibition is a race between a go process which begins accumulating in response to the imperative stimulus (i.e., the target reaches a critical point in its trajectory (Marinovic et al., 2009)), and a stop

process which accumulates in response to the stop-signal (i.e., the switch to daytime).

We empirically verified the applicability of the independent race model with four key observations (Verbruggen et al., 2019). Firstly, failures to stop should be earlier than responses on go trials because the stop process cuts off the upper tail of the go initiation time distribution (Fig. 3.2A). Secondly, if longer SSDs handicap the race in favor of the go process, the probability of correctly inhibiting should increase with shorter SSDs (Fig. 3.2B). Similarly, failed stop movement amplitudes should increase with longer SSDs because movements will be interrupted later in their course (Fig. 3.2C). Finally, taken together, stop failures should be earlier with shorter SSDs because only the quickest go processes can outrace the earliest accumulating stop processes (Fig. 3.2D). Having confirmed these assumptions empirically, we can be confident in our estimates of SSRT derived from it. In our interceptive stop-signal task, the mean SSRT was 197ms ($n = 50$, 95%C.I. = 13.3ms).

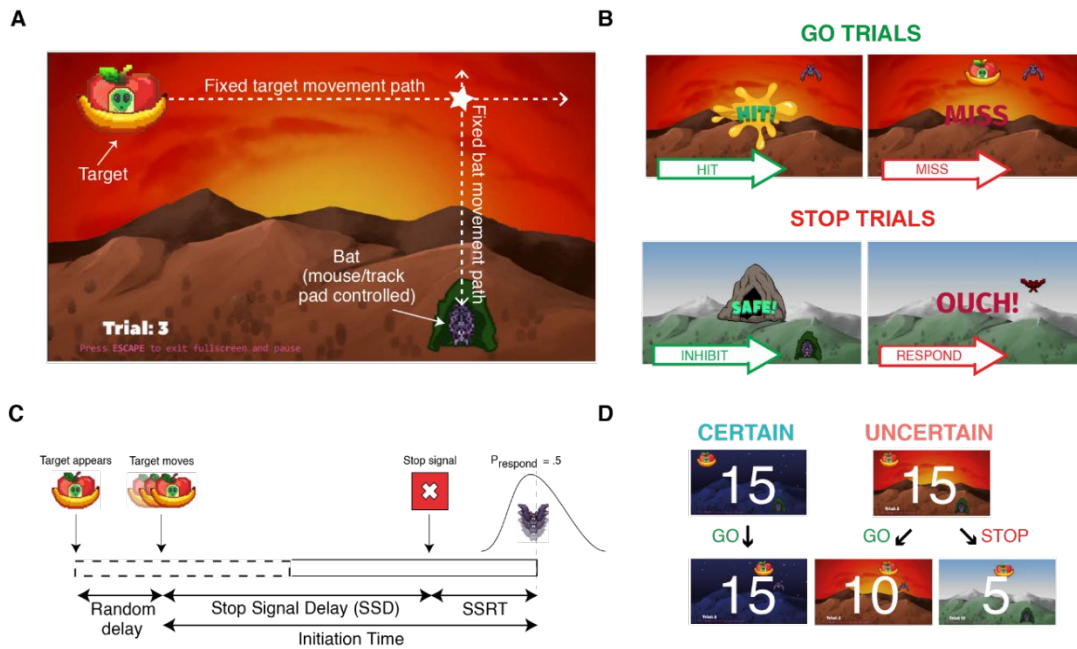


Figure 3.1. Task Schematic. (A) The target appears in the top-left of the screen. After a random delay, it moves from left to right. (B) On Go trials, participants try to hit the target with the bat. Feedback on hit success was given after the movement. On Stop trials, a stop-signal was denoted by the scene switching to daytime. Feedback was given depending on whether movement was successfully inhibited. (C) The Stop-Signal Reaction Time (SSRT) was calculated from estimates of the mean initiation time on Go trials and the SSD at which the probability of successfully inhibiting a movement was 0.5. (D) Experimental Blocks. Each block comprised 15 Certain (night) and 15 Uncertain (dawn) trials. There were 8 blocks, yielding 240 trials total. Within each block, the order of trials was random. Uncertain trials were used to estimate SSRT. The difference between initiation time, movement time, and timing error, on Certain and Uncertain Go trials, comprised our measures of proactive inhibition. At the end of the task, after all movement trial blocks, participants reported where the target was when they initiated movement, and where they aimed to hit the target, for both the Certain and Uncertain conditions.

These findings, in addition to the summary statistics presented in Table 1 (Verbruggen et al., 2019), give us confidence in the validity of our SSRT estimates. Nevertheless, delays to initiation can bias estimates of SSRT. Considering the average of binned estimates of SSRT in two blocks (Verbruggen, Chambers, & Logan, 2013), our estimate of the mean SSRT was 197ms(± 13.7) and not significantly different from the original estimate ($t(49) = -.581, p = .564$). Additionally, mean go-trial responses times can be earlier than incorrect responses on stop-trials they immediately precede,

particularly at the shortest SSDs (Bissett, Jones, Poldrack, & Logan, 2021). In our task, however, mean initiation times on stop-trials were quicker than on go-trials at all SSDs (Supplement C). In summary, the independent race model of inhibition holds. We can be confident participants performed the task as intended, thus movements on go-trials could be suitably constrained by the uncertainty of whether a stop-signal would be presented (Verbruggen & Logan, 2009).

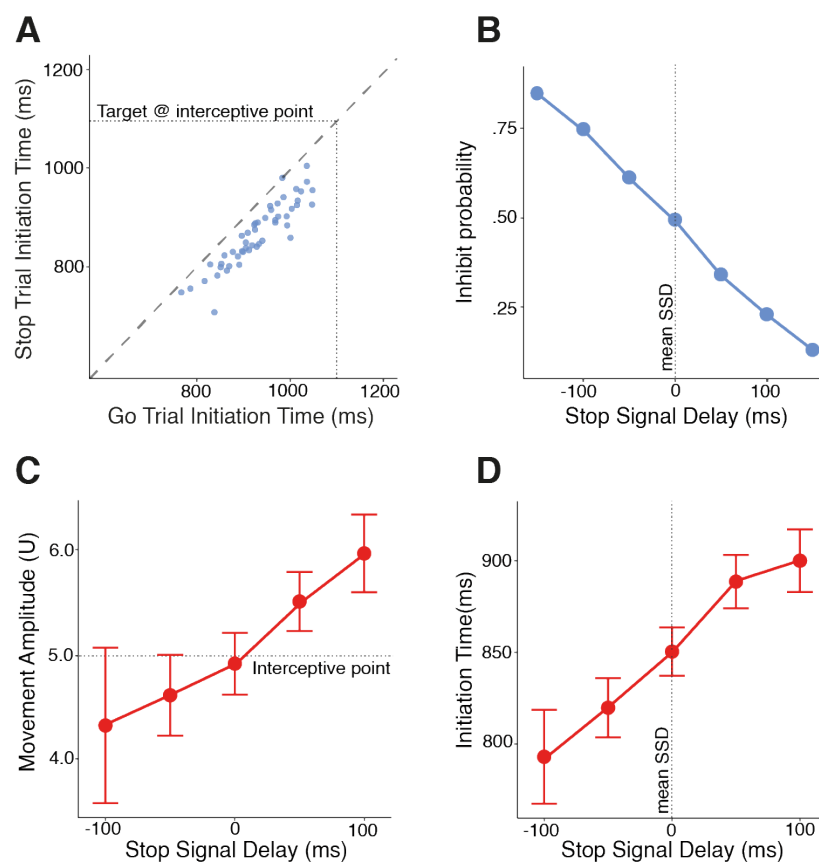


Figure 3.2. Empirical verification of the applicability of the independent race model. (A) Initiation times on go trials were longer than initiation times on failed stop trials for all participants. Each blue dot represents a single participant. The oblique, dashed line of equilibrium shows where initiation times would be equal. (B) The probability of correctly inhibiting decreases with longer stop-signal delays. Each blue dot represents the proportion of trials inhibited from the total at each level of stop-signal delay. (C) The amplitude of incorrect movements on stop trials increases with longer stop-signal delays. (D) Initiation times on failed stop trials increased with longer stop-signal delays. To allow direct comparison, stop-signal delays have been centred for each participant by subtracting their mean SSD. For panels (C) and (D) each red dot represents the population mean at each level of stop-signal delay, with error bars representing 95% confidence intervals.

Table 3.1. Summary statistics of measures used to calculate stop-signal reaction times

	Mean	SD	n
Probability of no response on go-trials	.021	.021	50
Probability of hitting target on go-trials	.924	.064	50
Initiation Time on go-trials (ms)	931	69.4	50
Probability of inhibiting on stop-trial	.500	.037	50
Nth trial	39.5	2.96	50
Mean stop-signal delay (ms)	738	88.5	50
Stop-signal Reaction Time	197	46.9	50

3.2.2. Stop-signal uncertainty led to briefer movements with delays to initiation and arrival

We assessed the effects of stop-signal uncertainty on interceptive movements. In our task, participants were told it was always safe to leave the cave at night (Certain), whereas the sun may come out at dawn (Uncertain) and movement should be withheld if it does. Each block consisted of 15 Certain (15 go-) and 15 Uncertain (10 go-, 5 stop-) trials and there were 8 blocks in total for 240 trials (Fig. 3.1D). The order of trials was pseudo-randomized within block such that Certain, Uncertain, and stop/go trials were approximately evenly distributed. Subsequently, the same seed was used for randomization such that all participants experienced the same order. Thus, we compared movement characteristics between Certain and Uncertain go-trials to ascertain the effects of proactive inhibition.

Our task yielded three measures of proactive inhibition: initiation time; movement time; and timing error. Initiation times were converted to time to

contact (TTC) values by subtracting the observed initiation time from the time taken for the target centre to reach the interceptive point (i.e., 1100ms). Larger values of TTC therefore represent initiations that are earlier in the target's trajectory, and any discrepancy between TTC initiation time and movement time will result in a timing error of equivalent size. All three measures of proactive inhibition demonstrated non-linear changes over the course of the experiment (Fig. 3.3A). Accordingly, 3-parameter exponential models were fit for each measure that allowed the intercept and asymptote to vary by Certainty (with random slopes and intercepts on both parameters). Contrasts were performed on mean estimates produced by the models by Certainty for each participant, with the intercept approximating performance at the start of the experiment and the asymptote approximating performance at the end. Thus, we were able to quantify proactive inhibition by considering differences in initiation time, movement time, and timing error between Certainty conditions, at the start and end of the experiment.

Initiation was delayed in response to stop-signal uncertainty ($F(1, 49) = 202.56, p < .001$), and as the experiment progressed ($F(1, 49) = 81.54, p < .001$). The interaction ($F(1, 49) = 18.58, p < .001$) suggests participants delayed more in the Uncertain condition as they went on (Fig. 3.3). Considering the differences, participants initiated $95(\pm 16)$ ms later in Uncertain relative to Certain conditions at the beginning of the experiment, and $134(\pm 21)$ ms later by the end (Fig. 3.3A).

Movement time was similarly affected by uncertainty ($F(1, 49) = 159.39, p < .001$) and progress ($F(1, 49) = 25.24, p < .001$). There was also an interaction ($F(1, 49) = 4.78, p = .034$) indicating participants shortened

movement times less in Uncertain conditions over the course of the experiment (Fig. 3.3). In terms of the overall difference, participants moved $44(\pm 7)$ ms quicker in Uncertain relative to Certain conditions, which diminished to $33(\pm 8)$ ms by experiment end (Fig. 3.3A).

The shortening of movement time was not sufficient to preserve timing error, given the delays to initiation. Indeed, there were effects of Certainty ($F(1, 49) = 193.36, p < .001$) and progress ($F(1, 49) = 81.11, p < .001$) on timing error, and an interaction between the two ($F(1, 49) = 32.88, p < .001$) such that participants delayed arrival more in Uncertain conditions as the experiment progressed (Fig. 3.3A). Proactive differences derived from the mean estimates show participants initially arrived $54(\pm 10)$ ms later to the target in the Uncertain condition, which increased to $99(\pm 16)$ ms over the course of the experiment (Fig. 3.3).

To be sure, we additionally considered a model-free analysis comparing participant means of each measure from the first and last experimental block. Mean and model estimates of proactive differences in initiation time, movement time, and timing error, at both the start and end of the experiment, were indistinguishable (Fig. 3.3B). In summary, participants delayed initiation and shortened movement time in response to stop-signal uncertainty, but the movement time shortening was not sufficient to preserve timing error and participants arrived later to the target. These differences were greater at the end of the experiment, with later initiation accompanied by less shortening of movement time, producing later arrival to the target in Uncertain conditions.

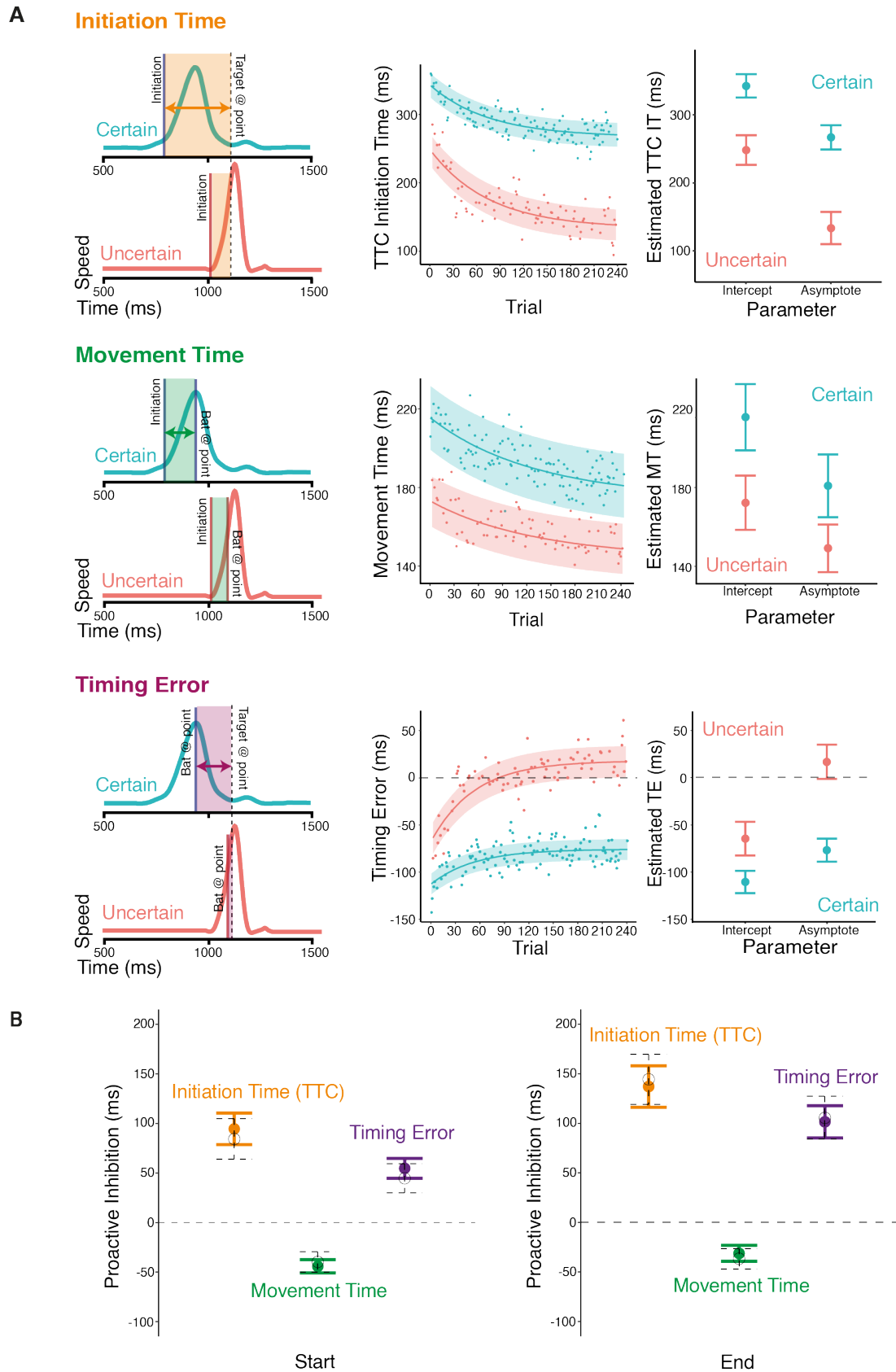


Figure 3.3. Measures of proactive inhibition. A) Quantifying the effects of stop-signal uncertainty on interceptive movements by comparing kinematic measures between Certain (blue) and Uncertain (red) conditions. Top: (Left) Velocity-time profiles of

representative movements in each condition. The initiation line indicates when the movement was initiated (i.e., displaced 0.7U), the bat at point line represents when the bat reaches the interceptive point (i.e., displaced 5U), and the target at point line represents when the center of the target would reach the interceptive point (i.e., after 1100ms). The colored/shaded areas represent the time elapsed for each measure. TTC Initiation Time (orange) is the time elapsed from initiation until the center of the target would reach the interceptive point. Movement Time (green) is the time elapsed from initiation until the bat crosses the interceptive point. Timing Error (purple) is the difference in time between when the bat reaches the interceptive point and the center of the target would reach the interceptive point (negative is earlier, positive is later). (Middle) 3-Parameter asymptote model fits for each measure. Individual points represent the observed population mean for each trial. Solid lines are estimates of the mean, with the shaded area representing 95% confidence intervals. (Right) Mean estimates of intercept and asymptote parameters by certainty. Points represent population mean, with error bars indicating 95% confidence interval. B) Each measure of proactive inhibition represents the difference in timing between Certain and Uncertain conditions. Coloured dots (error bars) represent the mean (95% confidence interval) of estimates extracted from our model parameters for each participant. Participants delay their initiation and quicken their movement in response to stop-signal uncertainty. Movements are not sufficiently quicker to preserve timing error, thus arrival to the target is also delayed. Delays to initiation and arrival are more pronounced at the end of the experiment. Black dots (dotted lines) show the mean (95% confidence interval) of participants' model-free proactive differences which are not statistically different from our model estimates.

3.2.3. Participants were explicitly aware of proactive changes to their movements

We found participants delayed their movement initiation and their arrival to the target in response to stop-signal uncertainty. But does this represent a volitional strategy? In motor control studies self-reported measures of intent are commonly used to quantify the extent changes in behavior are governed by explicit processes (Bond & Taylor, 2015; Taylor, Krakauer, & Ivry, 2014). In our task, the interceptive point is fixed, and the target moves at a constant speed. Accordingly, initiation time can be expressed spatially in terms of the position of the target at movement initiation, and timing error in terms of where the center of the bat strikes the target (Fig. 3.4A). To assess whether delays to initiation and arrival were volitional, we ran three additional assays

immediately following the experiment. In the first assay, participants watched a dummy Certain (counterbalanced Uncertain) trial and were asked to drag the target to where it would have been when they intended to leave the cave. For the second assay, the target appeared in the center of the screen and participants were asked to click where on the target they intended to hit. In a final assay, participants indicated where on the bat they were intending to hit the target. This enabled us to center the reported position on the target relative to the center of the bat for analysis. The same procedure was then repeated for the Uncertain (counterbalanced Certain) condition.

Considering initiation, participants reported the target had travelled further before intending to initiate in Uncertain relative to Certain conditions ($t(48) = 3.53, p < .001, d = .50$). Specifically, the target had travelled $3.34(\pm .48)U$ in the Uncertain condition compared to $2.22(\pm .54)U$ when Certain (Fig. 3.4B). Considering arrival, participants also reported intending to hit further to the rear of the target in Uncertain conditions ($t(48) = 3.03, p = .004, d = -.43$), with a mean bat-centred x-coordinate of $-.14(\pm .23)U$ compared to $.26(\pm 0.18)U$ when Certain (Fig. 3.4C). There was no difference in the reported y-position ($t(48) = .66, p = .514$).

Finally, to consider the extent to which explicit processes were responsible for the observed behaviour, we converted observed differences in initiation time and timing error at the end of the experiment into spatial units and compared them to the differences reported in the spatial assay (Fig. 3.4D). We observed the target having moved $1.47(\pm .23)U$ further prior to initiation in Uncertain conditions, whereas there was a reported mean difference of only $1.13(\pm .64)U$. Furthermore, we observed participants

arriving $1.08(\pm .18)U$ further to the rear of the target in Uncertain conditions, whereas the reported difference was only $.41(\pm .27)U$. Thus, the relative magnitudes of the explicitly reported strategies matched the observed behaviour, with participants reporting delaying their initiation more than their arrival, but the absolute magnitude of these effects was diminished compared to what was observed (Fig. 3.4D).

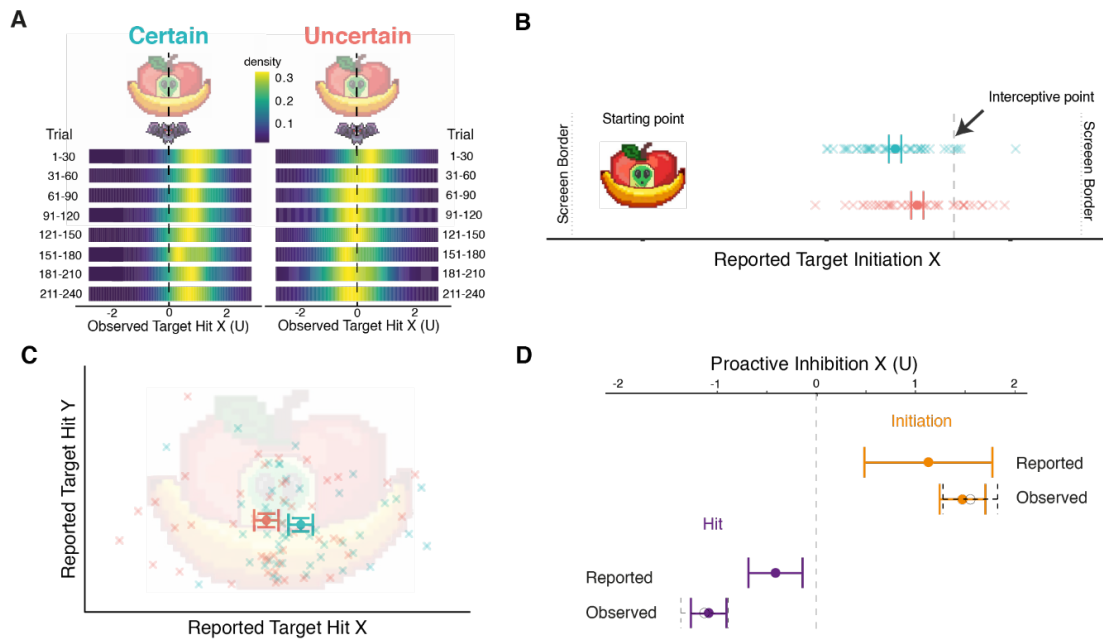


Figure 3.4. Spatial representation of observed timing errors and explicit reports of aiming strategies. A) Density plots of observed target hit x-coordinates relative to the center of the bat. In Certain conditions participants arrived at the front half of the target throughout the experiment. In Uncertain conditions, participants drifted towards the back half as the experiment progressed. B) Reported positions of target when participants initiated in Certain (blue) and Uncertain (red) conditions. Each cross represents a single participant, the dots (error bars) are the group means (95% within-subject adjusted CIs). Participants reported initiating when the target had travelled significantly further in the Uncertain condition. C) Reported position of where participants aimed to hit the target in each condition (normalized by reported bat position). Each cross represents a single participant, the dots (error bars) are the group means (95% within-subject adjusted CIs). Participants reported aiming significantly further to the back of the target in Uncertain conditions. D) Comparison between reported and observed differences in target initiation and arrival. For reported measures, dots (error bars) show mean spatial difference (95%CI) in reported initiation and hit between certainty conditions. For observed differences, coloured dots (error bars) show the mean difference (95%CI) from model estimates of initiation time (orange) and timing error (purple) at the end (i.e., the asymptote) of the experiment. Black dots (error bars) show the model-free mean differences

(95%CI) observed in the final block. Positive (negative) values represent a target/hit position further to the right (left) in Uncertain conditions for initiation/arrival respectively. Participants reported delaying their arrival less than they delayed their initiation which corresponds to observed behaviour. Nevertheless, the differences observed were greater in magnitude than both reported measures.

3.3. Discussion

Using a novel stop-signal task in which participants hit moving targets, we were able to probe the mechanisms underlying proactive inhibition. To our knowledge, this is the first time proactive changes to movements have been considered beyond the timing of their initiation with simple button presses. We found delays to initiation were accompanied by shortened movement times and delayed arrival, suggesting both response suppression and response delay contributed. Moreover, participants reported strategies reflected this behaviour, though did not fully account for the behaviour. This suggests both explicit and implicit processes were responsible for proactive stopping.

Firstly, we validated our task, finding the assumptions made by the independent race model were met (Fig. 3.2A-D). In our task, a natural limit to initiation delays was enforced by having to hit a moving target. Thus it is likely we additionally avoided bias and faster preceding go-trials because they are mitigated by capping movement onset delays (Bissett et al., 2021; Verbruggen et al., 2019). The average stop-signal reaction time was 197ms. This lies well within the measurement error of previous estimates in an interceptive timing context (Marinovic et al., 2009) and aligns with the ~200ms range observed in choice and simple response tasks. It should be noted it is considerably longer than the ~150ms observed in anticipation

timing tasks involving button presses (Leunissen, Zandbelt, Potocanac, Swinnen, & Coxon, 2017). This likely reflects the fact movements must be prepared further in advance when the movement time must be specified, with greater difficulties associated with inhibiting movements further in the preparatory stages (Marinovic et al., 2009). Given the empirical assumptions were met and our estimates of SSRT were sensible, we are confident participants were performing the task as intended and our estimates of reactive and proactive inhibition are thus valid.

Secondly, we considered proactive changes to the planning and execution of goal-directed movements. Under the uncertainty of whether a stop-signal could be presented, movement initiation was delayed. This has been previously observed in choice decision (Chikazoe et al., 2009; Jahfari, Stinear, Claffey, Verbruggen, & Aron, 2010; Verbruggen & Logan, 2009) and anticipation timing (Vink et al., 2015; Zandbelt et al., 2013; Zandbelt & Vink, 2010) contexts in which responses are recorded using simple button presses. Such proactive inhibition has been attributed to response suppression through activity in the circuitry responsible for reactive inhibition in anticipation of needing to stop (Aron, 2011). An alternative explanation is that delays in our task simply reflected a “waiting strategy” in which participants delayed the facilitation of their response, withholding movement until certain a stop-signal would not be presented (Rieger & Gauggel, 2002).

The present study addresses this controversy by considering the movement time and timing error associated with delayed onset of the response. In the pre-programmed model of interception, the movement time is programmed immediately prior to the go signal triggering (Marinovic et al.,

2009; James R. Tresilian, 2005). Therefore, if response suppression is implemented as an increase in the signal completion threshold (Verbruggen & Logan, 2009), movements will not be brief enough to preserve timing error because the movement duration cannot be updated once the plan has been triggered. Alternatively, any delays in facilitation can incorporate briefer movements because, by definition, they are triggered later.

In response to stop-signal uncertainty, we observed both briefer movements and delayed arrival, implying delays to initiation were achieved through a combination of a waiting strategy and response suppression. At the beginning of the experiment, these changes accounted for approximately equal proportions of the ~100ms initiation delay (~45ms briefer and ~55ms later in arrival). By the end of the experiment, however, the ~135ms initiation delay was offset by only ~35ms briefer movements, with arrival delayed by ~100ms. These data show, using these experimental parameters, waiting strategies were largely fixed over the course of the experiment, whereas suppression could be adapted between trials in response to feedback about performance, permitting even greater delays to initiation over many repetitions. Of course, whether this represents the general case remains to be seen. With faster and narrower targets, for example, there would be less of a timing window in which it was possible to hit the target, necessitating less variability in the end point error (J. R. Tresilian & Lonergan, 2002; J. R. Tresilian, Plooy, & Carroll, 2004; James R. Tresilian, 2005). This may eliminate the ability to effectively suppress or delay the response and still successfully hit the target.

In balance, our findings align with previous studies that favour response suppression as the mechanism driving delayed onset (Cai et al., 2011; Jahfari et al., 2010), particularly as it pertains to increased delays over the course of the experiment (Verbruggen & Logan, 2009). Making the distinction between delays and suppression has important implications. Future research in clinical populations may more accurately characterise the cognitive deficiencies in neuropathologies such as Parkinson's and ADHD, providing new insights into their development and treatment.

Of course, it is also possible that certain features of our task may have biased participants towards later arrival without suppressing the response. For example, having been trained to move with a minimum movement time of 100ms, perhaps participants were conditioned not to shorten duration any further. We believe this is unlikely because at their quickest, participants were not close to approaching this limit (Fig. 3.3A), and there was no penalty or feedback in the event the limit was exceeded. Rather than not being able to shorten movement times, however, it could be simply that they did not need to. There was a relatively large timing window of approximately 400ms, thus it was not necessary to account entirely for the delay in initiation because it was also possible to delay the estimate of the moment of interception and still hit the target. While this has some merit, it does not explain why participants did not both aim later and shorten their movement time further, permitting greater delays to movement onset and further improvements to successful inhibition. On the other hand, the presence of response suppression does place a limit on the quickening of movement, because the movement duration must be long enough to hit the target in

Certain conditions when initiation is earlier and the target is not directly “overhead”.

Finally, we considered whether these proactive changes were volitional. Our spatial assay allowed participants’ awareness of movement changes in movement planning to be quantified. In Uncertain conditions, participants reported initiating when the target was later in its trajectory (Fig. 3.4B) and aiming further to its rear (Fig. 3.4C). This supports the notion proactive inhibition is under volitional control (Aron, 2011; Jahanshahi et al., 2015; Verbruggen & Logan, 2009) because deliberate processes should be explicitly retrievable. However, we cannot entirely discount this was an explicit insight developed when questioned afterwards (Hadjiosif & Krakauer, 2021). For example, the assay may have prompted retroactive retrieval of visual cues that coincided with performance, rather than the proactive strategy guiding it.

Still, an interesting feature was that self-reported measures were smaller in magnitude than their observed counterparts (Fig. 3.4D). It is known that visual working memory for spatial estimates decays over time, with a reduction in the amplitude of spatial estimates when probed at increasing delays (Sheth & Shimojo, 2001). A reduction in magnitude of reported initiations and arrivals may simply reflect the fact participants were probed after the experiment concluded. This explanation is not entirely supported by the data, however, because there was no difference in reports between the counterbalanced orders of Certainty conditions, despite more time having elapsed once participants reported their second condition. It is therefore unlikely these reports simply reflected memory retrieval decay.

Assuming reports were of volitional strategies, it begs fundamental questions about the nature of the inhibitory process. For example, the underestimation of self-reported aim in reaching tasks has been accounted for by postulating an additional, implicit process that acts additively to produce the observed behaviour (Bond & Taylor, 2015; Morehead, Taylor, Parvin, & Ivry, 2017). Analogously, proactive inhibition may be further reduced into implicit and explicit components. Specifically, there may be a categorical decision to implement a compensatory strategy whose details are implicitly tuned with experience (e.g., one may decide to delay initiation and adjust the magnitude of that delay based on feedback). While previous work has indirectly assessed the assumption that proactive inhibition is volitional and under conscious control (Verbruggen & Logan, 2008), our method is the first to quantify it, providing an avenue for disentangling the contributions of explicit and implicit processes underlying proactive inhibition. Indeed, given that we found response delay was relatively fixed, with an increase in response suppression over the course of the experiment, future research should consider the extent to which the division of implicit and explicit processes may follow these distinct dimensions.

In conclusion, these results demonstrate that in contexts where there is uncertainty over whether a movement needs to be withheld, there are proactive changes to the planning and execution of that movement beyond onset delay. In the context of timed interception, we found both shortened movement times and later arrivals, suggesting a combination of delayed facilitation and response suppression contributed. This has important implications for our understanding of inhibition because while the amount of

inhibition will be correlated to onset delays in simple button press tasks, we have shown the degree to which response suppression and facilitation contribute is context dependent. Moreover, through quantifying the extent to which these changes were governed by explicit processes, we found participants were aware of both initiating and arriving later, but this did not account entirely for the difference observed. At bat, therefore, successful inhibition in response to an errant pitch may be augmented by a combination of delays and suppression to the planning and execution of the swing, improving the chances of detecting a need to stop. While this is underlain by explicitly retrievable processes, the extent to which this is the case, and how this corresponds to the underlying mechanisms, are important questions raised for future research.

3.4. Materials and Methods

3.4.1. Participants

Sixty participants were recruited from Prolific, an online recruitment platform. All participants resided either in the UK or US, had English as their first language, and had a minimum Prolific approval rate 95%. Participants received £3.50 upon successful completion of the study, which took approximately 25 minutes to complete. Pay was contingent on completion and not performance. Three participants were omitted because they had more than 5 trials missing from their data. Additionally, as an online study, we set stringent screening requirements to ensure all participants included in the final sample completed the task as intended. Specifically, they had to hit

more than 80% of targets in each condition, more than 80% of trials had to feature movement times less than 300ms, their probability of responding to a stop-signal must be between 40% and 60%, and the probability of omitting an appropriate go response must be less than 10%. Seven participants were excluded at this stage (4 for hit performance, 2 for elevated probability of stopping, and 1 for omitting too many go responses). Thus, the final sample for analysis was comprised of 50 participants (23 female, 4 left-handed, $\text{Mean}_{\text{age}} = 30.56$, $\text{SD}_{\text{age}} = 9.90$). The study was approved by the School of Psychology Ethics Committee at the University of Leeds (Reference: PSYC-116; Date: 27/10/2020).

3.4.2. *Experimental Task*

Participants completed a browser-based game, *Fruit Bat Splat*, in which they had to hit targets moving across a screen with a bat that was controlled by the movement of their mouse or trackpad. The game was programmed in Unity (ver. 2019.4.4f1) and implemented in WebGL. Participants were not required to use standardized screen resolutions, sizes, or refresh rates. Accordingly, dimensions (in brackets) are given in Unity units (U). Unity units scale with the resolution of the screen. A reference resolution of 1920x1080 was used with screen dimensions of 17.75Ux10U with 1U corresponding to 108 pixels. Screens that were not native 16:9 were letterboxed to preserve the dimension of their longest side. Coordinates are defined with (0,0) at the center of the screen. Fullscreen was forced and the mouse pointer locked and hidden at the center of the screen throughout the experiment.

The position of the cursor was represented on screen by a pixel art fruit bat (1.75Ux1.5U), which had a fixed x-position of 5.5U but could move freely in the y-plane (Fig. 3.1). The bat's wings were animated to improve participant engagement. Each flight cycle was comprised of four sprites: wings down, wings level, wings up, wings level. Each cycle lasted 20 frames (5 for each sprite). At the start of each trial, a start-zone represented by a pixel art cave (2.5Ux2.5U) appeared at the bottom right of the screen (5.5U, -4.5U). Participants were instructed to move the bat into the cave and click once. Subsequently, the bat snapped to the center of the start-zone and the flight animation was replaced with a static resting sprite, a bat hanging upside down from its feet inside the cave. On the same frame update, a target (3Ux2.25U) - depicted as a pixel art alien commandeering an Unidentified Fruity Object (UFO) – began to appear in the upper-left of the screen (-6.5U, 3.5U). The appearance of the UFO was animated, so that it was fully visible after 350ms. After a short pause, randomly drawn from a uniform distribution (500-1500ms), the target began to move along the x-axis towards the vertical plane of the bat at 10U/s. The interceptive point, where the center of the target crossed the x-position of the bat, was in the upper-right of the screen (4.5U, 2.5U). The target reached the interceptive point after it had moved 11U along the x-axis, the bat reached the interceptive point after it had travelled 5U along the y-axis (Fig. 3.1). The bat's flight animation would resume once it left the cave. If participants left the cave before the target began to move the target would disappear and the trial began again.

The study featured two certainty conditions: Certain and Uncertain (Fig. 3.1). On Certain trials, depicted by a task background of a mountain scene at night, participants were told it was safe for bats to leave the cave and to hit the target as it flew “overhead” (Certain Go-trials). On Uncertain trials, depicted by the same background mountain scene but at dawn, one third of trials presented a stop-signal before the target passed “overhead”. This was represented by the same scene instantly switching to daytime. Participants were told fruit bats burn easily in the sun and should try to withhold their movement in response to the stop-signal (stop-trials). But it was safe to leave the cave at dawn and to try to hit the target when a stop-signal was not presented (Uncertain go-trials). Uncertain trials were used to calculate our measure of reactive inhibition, Stop-signal Reaction Time (SSRT). Differences in *initiation time*, *movement time*, and *timing error* between Certain go-trials and Uncertain go-trials provide our three measures of proactive inhibition.

On go-trials, a successful hit could only occur if the upper edge of the bat contacted the lower edge of the target, indicated by a “HIT” graphic appearing in the center of the screen and accompanied by a splat sound effect. If the upper edge of the cursor moved past the lower edge of the target 1.5U before or after the center of the target had passed, the target stopped at that instant and a “MISS” graphic was displayed in the center of the screen. This prevented moving to the interception point early to “catch” the target.

On stop-trials, the stop-signal was first presented 320ms before the center of the target reached the interceptive point (i.e., a stop-signal delay of

780ms). This timing was derived from the mean stop-signal delay observed in a pilot study, ensuring the staircasing began near to the mean point at which movement is successfully inhibited 50% of the time. If the bat left the cave (i.e., displaced 0.75U), an “OUCH!” graphic appeared in the center of the screen, accompanied by a short animation of the bat being burnt in the sun and scorched sound effect. On the subsequent stop trial, the stop-signal delay was staircased 50ms shorter. If movement was successfully inhibited, a “SAFE!” graphic would appear in the center of the screen, accompanied by a cheerful chirping sound effect. On the subsequent stop trial, the stop-signal delay would be 50ms longer.

Feedback on all trials was displayed until participants clicked their mouse to advance to the next trial. For left-handed participants, the x-coordinates of the cursor and the target were reversed, with all sprites flipped horizontally.

3.4.3. Procedure

Prior to the experiment, participants indicated whether they were using a mouse or trackpad to control the cursor. Then they calibrated their cursor to ensure movements were approximately equivalent between individuals. Using a sensitivity slider, participants reported when a 5U displacement of the bat corresponded to a “single flick” (mouse) or “single vertical stroke” (trackpad). This mapping was subsequently used throughout the experiment.

Participants were then given step-by-step instructions on completing the task (Supplement A). To ensure movements were rapid, participants were trained to move at a movement time between 100ms and 300ms and

were unable to proceed to experimental trials until they had performed 5 successive movements within this movement time window. Participants were asked to move within this movement time window throughout the experiment, but this information was withheld so participants were not discouraged from delaying their responses and the effects of proactive inhibition could be observed.

Experimental trials were presented in 8 blocks of 30. Each block contained 15 Certain trials and 15 Uncertain trials. In Certain conditions, all 15 trials were go-trials. Of the Uncertain trials, 5 in each block were stop-trials and 10 were go-trials (Fig. 3.1D). The order of trials was randomized within each block. There were 240 trials in total. Participants were able to exit full screen, pause the game, and take a break at any time. Participants were unable to advance the experiment until they unpaused the game which once again forced full screen and locked the mouse pointer.

Following the main experimental blocks, we included two short tasks to investigate whether participants were explicitly aware of any differences in their movement characteristics between Certain and Uncertain conditions. Participants watched a simulated trial in which there was no bat to control, with either the Certain or Uncertain background. Before each trial, they were told to *“Pay attention to where the target is when you would leave the cave to hit it”* After the target travelled the full length of the screen it reappeared at its start point (-6.5U, 3.5U) with the instruction, *“Drag the UFO to the point you tried to leave the cave at [day/night]”*. Participants then dragged and dropped the target with their mouse to indicate where the target was when they initiated their movement. Next, the target and bat appeared in the center of

the screen along with the instructions “*Click the point of the UFO you tried to hit at [day/night]*” and “*Click the point of the BAT you were using to hit the UFO at [day/night]*” They clicked where on the target they were aiming to hit and where on the bat they were using to hit, respectively. The above was subsequently repeated with the alternate certainty condition. The order was counterbalanced with half the participants reporting Certain first. The movement initiation report always came before the aiming reports in both conditions.

All task code can be found in an online repository at:

<https://github.com/jpickavance/response-inhibition-game-unity-project>.

A demonstration version of the task can be found here:

<https://www.fruitbatsplat.com/demo>

3.4.4. Kinematic Analysis

All analyses were conducted after experimental data had been collected. Firstly, the position time series from each trial was resampled to a standard frequency of 100Hz. This is because Unity samples input at the same frequency as the monitor’s refresh rate which was beyond our control. 100Hz was chosen as the nearest round number between the most common framerates observed, 60Hz and 144Hz. We filtered the data using a zero-lag, 1st order, low-pass Butterworth filter with 20Hz cutoff. The *initiation time* (IT) was calculated as the initial time at which the bat had moved 0.75U (i.e., the lower most edge of the bat had crossed the center of the start-zone). When considering proactive inhibition only, initiation times were converted to time to contact (TTC) initiation times by subtracting the observed initiation time

from 1100ms. The resulting TTC initiation time thus expresses the time prior to the center of the target passing the interceptive point the initiation is made, with larger values earlier, and smaller values later in the target's trajectory. The *movement time* (MT) was calculated as the time elapsed from the initiation time to the point at which the bat crossed the interceptive plane. We used cubic interpolation on all positions of the center of the target and the center of the bat, from initiation time until max movement amplitude, to estimate the precise moment the bat's center intersected the interceptive plane (i.e., the y-position of the lowermost edge of the target). The *timing error* (TE) was calculated by dividing the displacement between the centers of the target and bat and dividing by the speed. Positive timing errors indicate the center of the bat arrived later than the center of the target, negative timing errors earlier.

3.4.5. Stop-signal Reaction Times

Stop-signal Reaction Times (SSRTs) were estimated from Uncertain trials only. They were calculated for each participant using the integration method. Initiation times on go-trials were ranked and the n th trial was found where n is the total number of go-trials multiplied by the probability of responding. Individuals' mean stop-signal delays (SSD) were subtracted from their go-trial initiation times on the n th trial to find their SSRT. This is suitable when using a staircasing procedure with at least 40 stop trials and their incidence is 33% or less (Matzke, Verbruggen, & Gordon, 2020). Trials on which go responses were incorrectly omitted were assigned the maximum initiation time observed (Verbruggen et al., 2019). Trials were then ranked according

to their initiation time. The n th IT was selected where n is the probability of responding given a stop-signal multiplied by the number of go responses observed. The SSRT was found by subtracting the mean stop-signal delay from the n th IT (Matzke et al., 2020). Actual values of the SSD were used to compute the mean (cf. programmed values) as the precise presentation of the stop-signal depended on the refresh rate of the display (Verbruggen et al., 2019). Summary statistics of the variables used to calculate SSRTs are displayed in *Table 3.1*.

3.4.6. Proactive Inhibition

Differences in *initiation time*, *movement time*, and *timing error*, on go-trials between Certain and Uncertain conditions represent our measures of proactive inhibition. Additionally, when considering the effects of proactive inhibition, we wanted to ensure participants were timing their initiations to move with ballistic movements. Accordingly, trials were removed in which participants initiated before the target had crossed the halfway point, after the target had left the screen, or with a movement time of more than 300ms. In total, 621/9896 (~6.3%) trials were removed at this stage.

Summary plots revealed each measure was characterized by a non-linear change that appeared to become asymptotic as trials progressed. Rather than take a single mean value for each participant, therefore, we modelled each dependent variable using a simple 3-parameter asymptote model:

$$y = \varphi_I + (\varphi_I - \varphi_A)e^{-\varphi_{LR}^{\text{trial}}}$$

Where φ_I is the y-intercept (i.e., value at beginning of experiment), φ_A is the asymptote (i.e., approximate value at end of experiment), and φ_{LR} is the learning rate. Prior to modelling, movement times were additionally transformed using a log transformation to normalize a positively skewed distribution.

To determine the significance of the effect of certainty at the start and end of the experiment, we began with a null model which computed the intercept on each parameter, with random intercepts for φ_I and φ_A for each participant. The effect of certainty on φ_A (i.e., the asymptote) was determined by constructing a model which additionally included the effect of certainty on φ_A with random slopes for each participant on φ_A . A likelihood ratio test was then performed between the two models and the p-value taken as the level of significance of the effects of certainty on φ_A (Winter, 2013). We additionally considered a third model, including the effects of certainty on φ_I (i.e., the intercept) and random slopes for each participant on φ_I . A likelihood ratio test was performed between this and the best performing, most parsimonious model thus far (i.e., the asymptote model if significant, the null model if not). Finally, we allowed φ_{LR} (i.e. the learning rate) to vary by certainty. Though we were primarily interested in estimating mean values at the start and end of the experiment (i.e., φ_I and φ_A), we wanted to ensure we had the most accurate estimates possible. Finally, this model was compared to the best performing model to point. Models were constructed using the *lme4* package in R studio (ver 3.6.0). Starting parameters were determined graphically. Optimisation was performed using the Broyden–Fletcher–Goldfarb–Shannon algorithm as implemented in the *optimx* package. The

best performing model for all three measures included random slopes and intercepts on ϕ_I and ϕ_A , but no effect of certainty on ϕ_{LR} . These comparisons can be found in Supplement B.

From the best model, individual fits for each participant were used to provide mean estimates for each dependent variable at the start and end of the experiment. We performed repeated-measures ANOVAs on these estimates to determine the significance of the effects of proactive control over the course of the experiment on each dependent variable. Shapiro-Wilk tests and qq-plots confirmed normally distributed data and variance for each of the contrasts. Prior to this, movement times were additionally transformed to their original scale by finding the exponent of the estimate. Individual model fits for each participant can be found in the supplementary materials. Finally, difference scores for IT, MT, and TE, were calculated per participant for each model, which represent our final measures of proactive control. The group means (95%CI) are displayed for each measure at both the start and end of the experiment in *Fig. 3.3B*. Finally, to compare these effect sizes to explicit reports, we transformed estimates of IT and TE into target position at initiation and arrival respectively by multiplying by a factor of .011 (i.e., the distance the target travelled in Unity units (U) in 1ms; *Fig. 3.4D*). All data are reported as mean $\pm$ 95%CI across all subjects.

3.4.7. Model-free analysis

We also considered the mean of each measure for each participant over the first 30 (start) and final 30 (end) trials to sense check our models. The group means (95%CI) are presented in *Fig. 3.3B* and *Fig. 3.4D* as black, hollow

dots (dotted lines). Differences between model and model-free estimates were negligible, though the modelled estimates provided more precision with smaller CIs. All data are reported as mean $\pm 95\%$ CI across all subjects.

3.4.8. *Reported Aim*

We had two explicit measures of proactive control in each condition.

Reported target position is how far the target had travelled when participants reported they tried to initiate their movement in each condition. *Reported target hit* is where on the target participants reported aiming to hit the target in each condition. The latter was centred by subtracting away the point of the bat they reported using to hit the target. One participant was omitted from this stage of analysis (failed to provide any data), with 49 participants considered in total. 2 x 2 mixed ANOVAs confirmed the certainty order in which participants reported their aiming strategy had no effect on either *reported target position* ($F(1, 47) = .026, p = .873$) or *reported target hit* ($F(1,47) = .738, p = .394$), nor did it interact with certainty ($F(1, 47) = .389, p = .535$; $F(1,47) = .537, p = .467$). Accordingly, data was combined, and paired sample t-tests were run on both dependent variables between the two certainty conditions. This was to determine whether participants were actively aware of adjusting their initiation or arrival in response to uncertainty. Difference scores between Certainty conditions for each participant were also calculated which are displayed at the group level in *Fig. 3.4D*. All data are reported as mean $\pm 95\%$ CI across all subjects.

3.5. References

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3.6. Supplementary Materials

3.6.1. Supplement A: Task Instructions

Instructions are given in italics

[requirement to advance is given in parentheses – if requirement is not met, trial repeats]

Main task training

1. *Use the mouse to move the cursor into the cave (blue/night background displayed - Certain Go-trial)*
[bat over cave]
2. *The cave turns green when the bat enters. CLICK the mouse to rest*
[click mouse]
3. *Keep still and wait for the target to fly closer*
[movement withheld]
4. *Wait for the fruit to fly over the cave. Try to hit it with the bat!*
[hit the target with the bat]
5. *The fruit won't always be this slow*
[click to advance feedback and cue a faster moving target]
6. *Try to hit the fruit again (Certain Go-trial)*
[hit the target with the bat]
7. *Fruit bats get tired: flying too fast OR flying too slow. Use the flight timer to help you avoid getting tired (Certain Go-trial)*
[hit the target with the bat and a movement time between 100-300ms]
8. **Movement time test.** *Hit the fruit. Move with a good flight time. Goal: 5 in a row (Certain Go-trial)*
[hit the target with a movement time between 100-300ms 5 times consecutively. Score is reset to zero after a movement quicker than 100ms or slower than 300ms]
9. **Movement time training passed.** *Congratulations, you have completed the first round of training! Your excellent performance means you will no longer have the flight timer to help you. The flight time will still be recorded so try to fly with a good flight time in all future rounds.*

[click mouse]

10. *Fruit bats easily sunburn. Stay inside the cave during the day (white/day background displayed)*
[movement withheld]
11. *Try to hit the fruit with a good flight time at night. Stay inside the cave at day*
[hit target on night trials, withhold movement on day trials – 3 of each in total]
12. *Fruit bats can still collect fruit at sunrise. Hit the fruit with a good flight time (background changes to red/dawn Uncertain Go-trial)*
[hit the target with the bat]
13. *At sunrise, it can turn to day. Stay inside the cave if it turns to day. (Uncertain Stop-trial with SSD of 580ms)*
[movement withheld]
14. **Stop signal test** *Hit the fruit with a good flight time at night. Hit the fruit with a good flight time at sunrise. Stay inside when it turns to day.*
[Randomly interleaved trials:
3 x Certain Go trials: hit the target with the bat
4 x Uncertain go trials: hit the target with the bat
4 x Uncertain Stop trials: withhold movement]
15. **Stop signal training passed.** *You have completed training. The rules are the same for the full game: Night- hit the fruit with a good flight time. Sunrise- hit the fruit with a good flight time. Day- stay inside the cave. There will be 240 trials in total. You will be graded on your performance at the end. Good luck!*

Warning messages during task

Movement > 300ms: *You moved too slow. Try not to leave the cave until you can hit the fruit with one smooth movement*

Movement withheld on go trial: *You did not move. Please try to hit the fruit at night and sunrise.*

Self-reporting initiation and aim instructions

1. *You will now see the UFO fly overhead. Pay attention to where the target is when you would leave the cave to hit it.*

[click ready]

2. *Drag the UFO to the point you tried to leave the cave at (day/night)*
[drag and drop UFO to point on screen and click submit]
3. *Click the point of the UFO you tried to hit at (day/night)*
[click on the UFO and then submit]
4. *Click the point of the BAT you were using to hit the UFO at (day/night)*
[click on the bat and then submit]

3.6.2. Supplement B: Modelling

3.6.2.1. Method

Summary plots revealed each measure was characterized by a non-linear change that appeared to become asymptotic as trials progressed. Rather than take a single mean value for each participant, therefore, we modelled each dependent variable using a simple 3-parameter asymptote model:

$$y = \varphi_I + (\varphi_I - \varphi_A)e^{-\varphi_{LR} \text{trial}}$$

Where φ_I is the y-intercept (i.e., value at beginning of experiment), φ_A is the asymptote (i.e., approximate value at end of experiment), and φ_{LR} is the learning rate. Prior to modelling, movement times were additionally transformed using a log transformation to normalize a positively skewed distribution.

To determine the significance of the effect of certainty at the start and end of the experiment, we began with a null model which computed the intercept on each parameter, with random intercepts for φ_I and φ_A for

each participant. The effect of certainty on φ_A (i.e., the asymptote) was determined by constructing a model which additionally included the effect of certainty on φ_A with random slopes for each participant on φ_A . A likelihood ratio test was then performed between the two models and the p-value taken as the level of significance of the effects of certainty φ_2 (Winter., 2013). We additionally considered a third model, including the effects of certainty on φ_I (i.e., the intercept) and random slopes for each participant on φ_I . A likelihood ratio test was performed between this and the best performing, most parsimonious model thus far (i.e., the asymptote model if significant, the null model if not). Finally, we allowed φ_{LR} (i.e. the learning rate) to vary by certainty. Though we were primarily interested in estimating mean values at the start and end of the experiment (i.e., φ_I and φ_A), we wanted to ensure we had the most accurate estimates possible. Finally, this model was compared to the best performing model to point. Models were constructed using the *lme4* package in R studio (ver 3.6.0). Starting parameters were determined graphically. Optimisation was performed using the Broyden–Fletcher–Goldfarb–Shannon algorithm as implemented in the *optimx* package.

3.6.2.2. Results

The initiation time asymptote was different across conditions of trial certainty ($\chi^2(4) = 3973.8$, $p < .001$), as was the parameter for initiation time at the beginning of the task ($\chi^2(5) = 227.1$, $p < .001$). The learning rate parameter was not significant ($\chi^2(1) = .035$, $p = .853$). Therefore, estimates for individuals' initiation times at the beginning and end of the experiment

were computed using the model with fixed and random effects of certainty on φ_I and φ_A .

Our fitted parameters for movement time were affected by the trial certainty ($\chi^2(4) = 1444.7$, $p < .001$) and this also affected our parameter for movement times at the start of the task ($\chi^2(5) = 260.1$, $p < .001$) but not the rate of change throughout the task ($\chi^2(1) = 1.51$, $p = .219$). We therefore used estimates of individuals' movement times at the beginning and end of the experiment using the model with fixed and random effects of certainty on φ_1 and φ_2 (Fig. 3.3).

The effect of certainty on the asymptote of timing error was significant ($\chi^2(4) = 2753.7$, $p < .001$). In addition, the effects of certainty on the intercept were also significant ($\chi^2(5) = 54.17$, $p < .001$). Moreover, the effects on learning rate did slightly improve the model ($\chi^2(1) = 4.06$, $p = .0439$). Thus, the effects of proactive inhibition were examined using estimates of individuals' timing errors at the beginning and end of the experiment using the model with fixed and random effects of certainty on φ_I , φ_A , and φ_{LR} (Fig. 3.3).

3.6.2.3. Individual fits

3.6.2.3.1. Initiation Time



3.6.2.3.2. Movement Time



3.6.2.3.3. Timing Error



3.6.3. Supplement C: Context Independence Violations

Recent work has shown that go-trial initiation times can be quicker than stop-trial initiation times when they immediately precede them (Brisset et al., 2021). To see whether this was a problem in our task, we grouped individuals' stop-trials by (centered) stop signal delay. Considering only the initiation times of the immediately preceding go-trial on stop-trials there was an incorrect response, we found mean initiation times were quicker on stop-trials than on immediately preceding go-trials for all SSDs with more than 10 pairs of responses (Fig. 3.1)

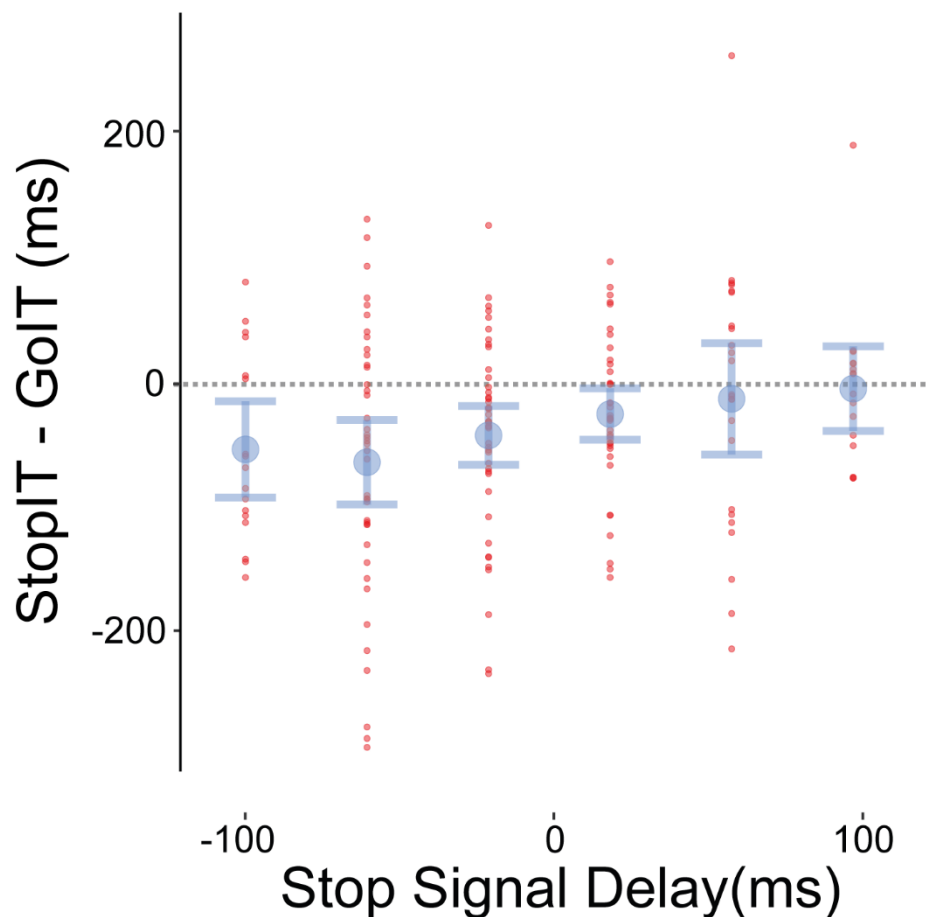


Figure 3.S1. Comparing the difference between stop-trial initiation times with go-trial initiations that immediately precede them. Red dots are participants average differences grouped by stop signal delay. Blue dots (error bars) represent the group mean difference(95% ci) at each stop signal delay. For the sake of direct

comparison, stop signal delays have been cantered for each participant by subtracting their mean SSD. Mean stop-trial initiation times are quicker, or no longer than mean go-trial initiation times at all levels of stop signal delay.

Chapter 4: Reactive and proactive inhibitory control in adolescents: a cross-sectional experimental study

Adolescence is a developmental period often characterised by a lack of self-regulation. This reduced self-regulation is associated with impulsive and risk-taking behaviors that subside with adulthood. A key determinant of self-regulation is the inhibitory control of action, and such inhibition is associated with the pre-frontal cortex (PFC). The PFC is known to mature over adolescence and into the third decade of life. Thus, the associations between adolescent impulsivity and PFC maturation paint a consistent picture of developmental change. However, experimental measures of inhibition do not match this pattern. Commonly used metrics typically show children reaching adult levels of performance at 12 years of age. We measured inhibition in an adolescent population using a stop-signal task in which adolescents ($n = 223$; ages 11-14 years) and adults ($n = 55$) attempted to hit moving targets with a bat. This allowed 'inhibition' to be separated into reactive and proactive components. We found that reactive inhibition reached adult levels by 11 years of age, but proactive inhibition was still improving at 14 years. Moreover, we included these metrics in models of adolescent mathematics attainment and found associations between proactive but not reactive inhibition. Our findings resolve the apparent contradiction between experimental, observational, and neurological measures of inhibitory control across the second decade of life. These results strongly indicate that future

studies of adolescence should include measures of proactive inhibition and suggest that such measures may help identify important risk factors within adolescent populations.

4.1. Introduction

While traditionally, infancy and early childhood attracted the interest of developmental scientists, in the last quarter century or so adolescence has started to receive much greater attention (Konrad, Firk, & Uhlhaas, 2013). Adolescence is marked by profound anatomical, behavioural, and emotional changes. This period of intense transition from childhood into adulthood is typically one prone to heightened risk-taking and recklessness (Steinberg, 2008). Imaging studies have revealed there is a profound reorganization of the brain, with increases in cortical white matter (i.e., connectivity) coinciding with decreases in grey matter (i.e., pruning) (Blumenthal et al., 1999). This development typically follows a course that is “back-to-front” (Gogtay et al., 2004), with sensorimotor areas first to mature, and the prefrontal cortex the last, with changes taking place well into the 20s.

The prefrontal cortex plays an important role in higher order cognitive control, most notably, in overriding actions when they would be inappropriate. Indeed, it is the relative immaturity of the prefrontal cortex through the mid stages of adolescence that may explain the difficulties in self-regulation (Jacobson, Williford, & Pianta, 2011), and the impulsive and risk-taking behaviors, by which adolescence is often characterised

(Blakemore & Choudhury, 2006; Casey, Jones, & Hare, 2008; Konrad et al., 2013).

Nevertheless, there is only marginal experimental evidence for any meaningful changes to metrics of inhibition through adolescence. Error-rates in go-no go (Tamm, Menon, & Reiss, 2002) and anti-saccade (Luna, Garver, Urban, Lazar, & Sweeney, 2004) tasks reach adult levels in childhood, and by the age of 12, at the very onset of adolescence, Stroop performance too has reached maturity (Leon-Carrion, García-Orza, & Pérez-Santamaría, 2004).

The gold standard measure of motor inhibition, stop-signal reaction time (Logan & Cowan, 1984), has shown some promise, with improvements reported up until the ages of 12-13 (Dupuis et al., 2019; Ridderinkhof, Band, & Logan, 1999; Williams, Ponesse, Schachar, Logan, & Tannock, 1999). But this too fails to align with observations of a subsidence in risk taking behaviors that are attributed to the maturation of prefrontal cortex well into the mid-20s.

However, one's ability to successfully inhibit movement in response to a command to stop, is not entirely determined by the reactive speed of the inhibitory process. By proactively and deliberately delaying the onset of the response, it is possible to elevate the probability of detecting the need to stop (Verbruggen & Logan, 2009). We hypothesize that it is this deliberate, proactive form of inhibition that continues to develop through adolescence as the pre-frontal cortex continues to mature.

This prediction is supported by growing experimental evidence that *proactive* modes of cognitive control only emerge ontogenically once there is

capacity for the active maintenance of goal-relevant information (Braver, 2012; Chevalier, James, Wiebe, Nelson, & Espy, 2014; Chevalier, Martis, Curran, & Munakata, 2015; Valadez et al., 2022). In sensorimotor contexts, that information can be knowledge of the latency of the inhibitory process itself. In checking a swing in baseball, for example, only when the physiological limits of reactive inhibition are reached and known, can preparations be made to maximally delay the swing and still strike the ball (Marinovic, Plooy, & Tresilian, 2009, Chapter 2). Given that the reactive process hasn't reached maturity until 12-13 years of age (Dupuis et al., 2019), therefore, it follows that we would expect proactive inhibition in this context to show signs of development beyond early adolescence. Indeed, this further aligns with imaging studies that show proactive stopping is implemented via fronto-striatal input (Adnan Majid, Cai, Corey-Bloom, & Aron, 2013), the connectivity strength of which increases until the age of 25 (Van Den Bos, Rodriguez, Schweitzer, & McClure, 2015).

The present study aims to address the current empirical gap between neural, observational, and experimental findings. To do this, we've developed a task to measure inhibitory processes in the context of interceptive actions (Chapter 3). This is a stop-signal task in which participants attempt to hit a target as it moves "overhead". This permits us to measure reactive inhibition as the latency of the stop process (i.e., stop signal reaction time). Moreover, comparing movement characteristics between (uncertain) conditions in which a stop-signal might appear to (certain) conditions in which stop-signals never appear, we can measure three dimensions of proactive inhibition: movement onset delay, movement

duration shortening, and movement endpoint delay. Comparing reactive and proactive inhibition metrics through early adolescence and adulthood, we aim to demonstrate which dimension(s) of inhibition continue to show signs of development into mid-adolescence. Additionally, by assessing the degree to which participants are aware of their proactive strategies using a self-reported assay upon task completion, we can determine the extent to which these strategies are volitional, and the point at which this emerges.

The importance of identifying suitable metrics for use with adolescent populations cannot be understated. Difficulties self-regulating and risk-taking behaviors that emerge in mid-adolescence can be life altering, often associated with poorer academic and clinical outcomes (Gutman & Vorhaus, 2012; Kipping, Campbell, MacArthur, Gunnell, & Hickman, 2012). If we wish to better identify at risk individuals, establish causal pathways, and intervene effectively, our experimental measures must bear some relation to the biological changes taking place and the real-world outcomes they affect.

The second part of the study addresses the real-world consequences of sensorimotor and inhibitory deficiencies. Previously, we found target hitting performance and inhibition independently predicted attainment in mathematics in children and adolescents (Chapter 2). The former aligns with a growing body of evidence pointing towards a common neural architecture shared between sensorimotor and mathematical operations (Anderson, 2010; Anobile, Arrighi, Castaldi, & Burr, 2020; Dehaene, Spelke, Pinel, Stanescu, & Tsivkin, 1999). Nevertheless, inhibition was only broadly construed, and it remains unclear whether *reactive*, *proactive*, or some combination of both domains were responsible for the association.

Thus, we included bonus blocks interleaved with the inhibition blocks, in which the target moved at different speeds to produce a metric of interceptive timing performance over a range of timing constraints. Subsequently, we were able to model mathematics attainment using interceptive timing performance and our inhibition metrics as predictors. We aim not only to scrutinize our previous result, but also to elucidate which dimension(s) of inhibition show promise as neurodevelopmental markers in the context of adolescent outcomes in mathematics.

4.2. Results

4.2.1. Adolescents met the assumptions of the independent race model of inhibition, proactively inhibited their movements, and exhibited typical behaviour in response to increased timing constraints.

We validated our task for use with an adolescent population empirically, considering whether sensible values of SSRT could be estimated, proactive inhibition was observed, and that interceptive actions were suitably constrained by increased timing demands.

In *inhibition* blocks, participants tried to hit a target as it moved “overhead” with a bat controlled by mouse (Fig. 4.1A). In Uncertain trials it was dawn (indicated by the color of the sky), and there was a 33% chance a stop-signal (indicated by an instant switch to daytime) could be presented. Participants tried to withhold movement in response to the stop-signal (stop-trial; Fig. 4.1B) and hit the target in its absence (go-trial; Fig. 4.1B). On the subsequent stop-trial, the stop-signal was delayed (cf. brought forward) 50ms if participants successfully inhibited (cf. incorrectly responded).



Figure 4.1. Task Schematic. (A+B) Inhibition blocks. (A) The target appears in the top-left of the screen. After a random delay, it moves from left to right. (B) Each block comprised 20 Certain trials and 30 Uncertain trials. In Certain conditions, all trials were go-trials in which participants tried to hit the target with the bat. In Uncertain conditions, there was a 1/3 chance the scene would change to daytime at a staircased delay and participants tried to withhold movement. (C+D) Bonus blocks. (C) scaled version of the target follows the same fixed trajectory over a white background. Participants used a scaled bat to hit the target moving at one of four different speeds. (D) Each bonus block comprised 12 trials at 4 different speeds. (E) Experimental session. Firstly, participants completed a minimum of 21 training trials to ensure they understood the instructions. Four inhibition blocks were then interleaved with four bonus blocks. Within each block, the order of trials was random. From the inhibition blocks, Uncertain trials were used to estimate SSRT. The difference between initiation time, movement time, and timing error, on Certain and Uncertain Go trials, comprised our measures of proactive inhibition. The total proportion of targets hit during the bonus blocks was our measure of interceptive timing performance. Finally, participants completed a self-report assay in which they reported where the target was when they initiated, where they aimed to hit the target, and where on the bat they hit the target, for both Certain and Uncertain conditions.

SSRTs were calculated using the integration method. These estimates rely on assumptions made by the independent race model of inhibition (Chapter 3 and Verbruggen et al., 2019 for further details). Firstly, failures to stop should be earlier than responses on go trials (Fig. 4.2A). Secondly, the probability of correctly inhibiting should increase with earlier SSDs (Fig. 4.2B). Thirdly, failed stop movement amplitudes should increase with later SSDs (Fig. 4.2C). Finally, stop failures should be earlier with earlier SSDs (Fig. 4.2D). Having confirmed these assumptions empirically, and with reference to the summary statistics presented in Table 4.1, we can be confident in our estimates for adolescent SSRTs. The mean SSRT among adolescents was 201ms ($n = 204$, 95% C.I. = 8.60ms).

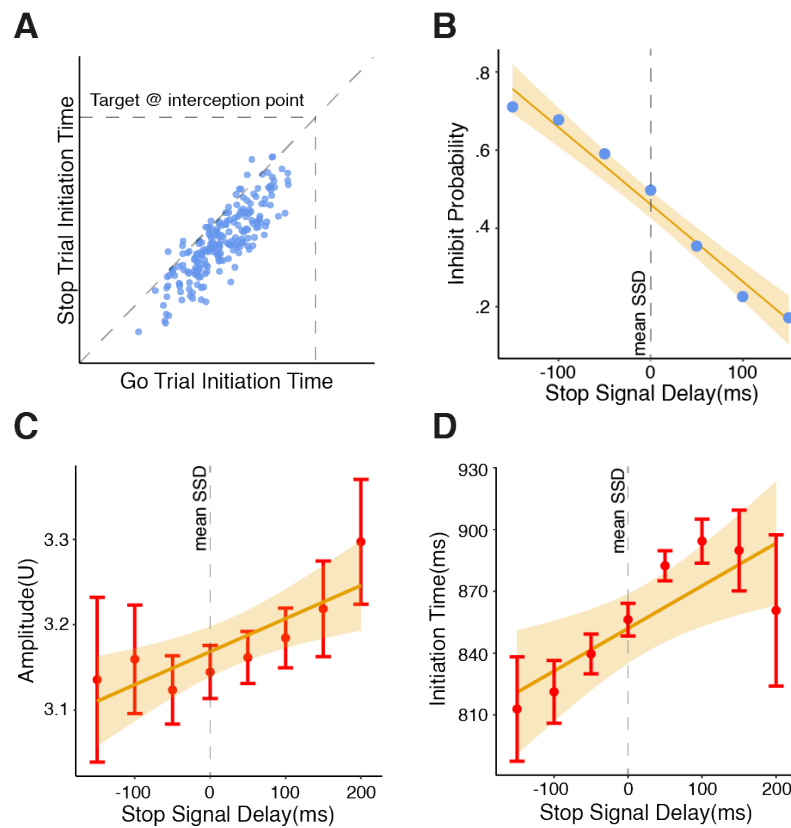


Figure 4.2. Empirical verification of the applicability of the independent race model. (A) Initiation times on go trials were longer than initiation times on failed stop trials for all but 12 participants, with the remainder falling within the margin for error. Each blue dot represents a single participant. The oblique, dashed line of equilibrium shows where initiation times would be equal, with the orthogonal dashed lines representing the time at which the target would cross the interception point. (B) The probability of correctly inhibiting decreases with longer stop-signal delays. Each blue dot represents the proportion of trials inhibited from the total at each level of stop-signal delay. (C) The amplitude of incorrect movements on stop trials increases with longer stop-signal delays. (D) Initiation times on failed stop trials increased with longer stop-signal delays. To allow direct comparison, stop-signal delays have been centred for each participant by subtracting their mean SSD. For panels (C) and (D), each red dot represents the population mean at each level of stop-signal delay, with error bars representing 95% confidence intervals. Additionally, for panels (B), (C), and (D), linear models have been superimposed to assist interpretation.

Table 4.2. Summary statistics of measures used to calculate stop-signal reaction times for years 7, 8, and 9.

	Mean	SD	n
Probability of no response on go-trials	.018	.017	204
Probability of hitting target on go-trials	.918	.044	204
Initiation Time on go-trials (ms)	916	61.1	204
Probability of inhibiting on stop-trial	.482	.037	204
<i>N</i> th trial	40.7	3.10	204
Mean stop-signal delay (ms)	704	102	204
Stop-signal Reaction Time	201	62.3	204

Certain trials (indicated by a night scene), in which participants were instructed to always hit the target, also appeared during the *inhibition* blocks. We compared movement characteristics between Certain go-trials and Uncertain go-trials (i.e., when the stop-signal did not appear) to ascertain whether there were any proactive changes to movement planning (Fig. 4.3A). Adolescents delayed movement initiation ($F(1, 203) = 275.80$, $p < .001$), shortened movement time ($F(1, 203) = 142.23$, $p < .001$), and arrived later to the target ($F(1, 203) = 213.49$, $p < .001$), in Uncertain relative to Certain trials. Moreover, there was an effect of time such that by the end of the experiment, adolescents were delaying initiation more ($F(1, 203) = 278.23$, $p < .001$), moving quicker ($F(1, 203) = 89.25$, $p < .001$), and arriving later to the target ($F(1, 203) = 141.40$, $p < .001$).

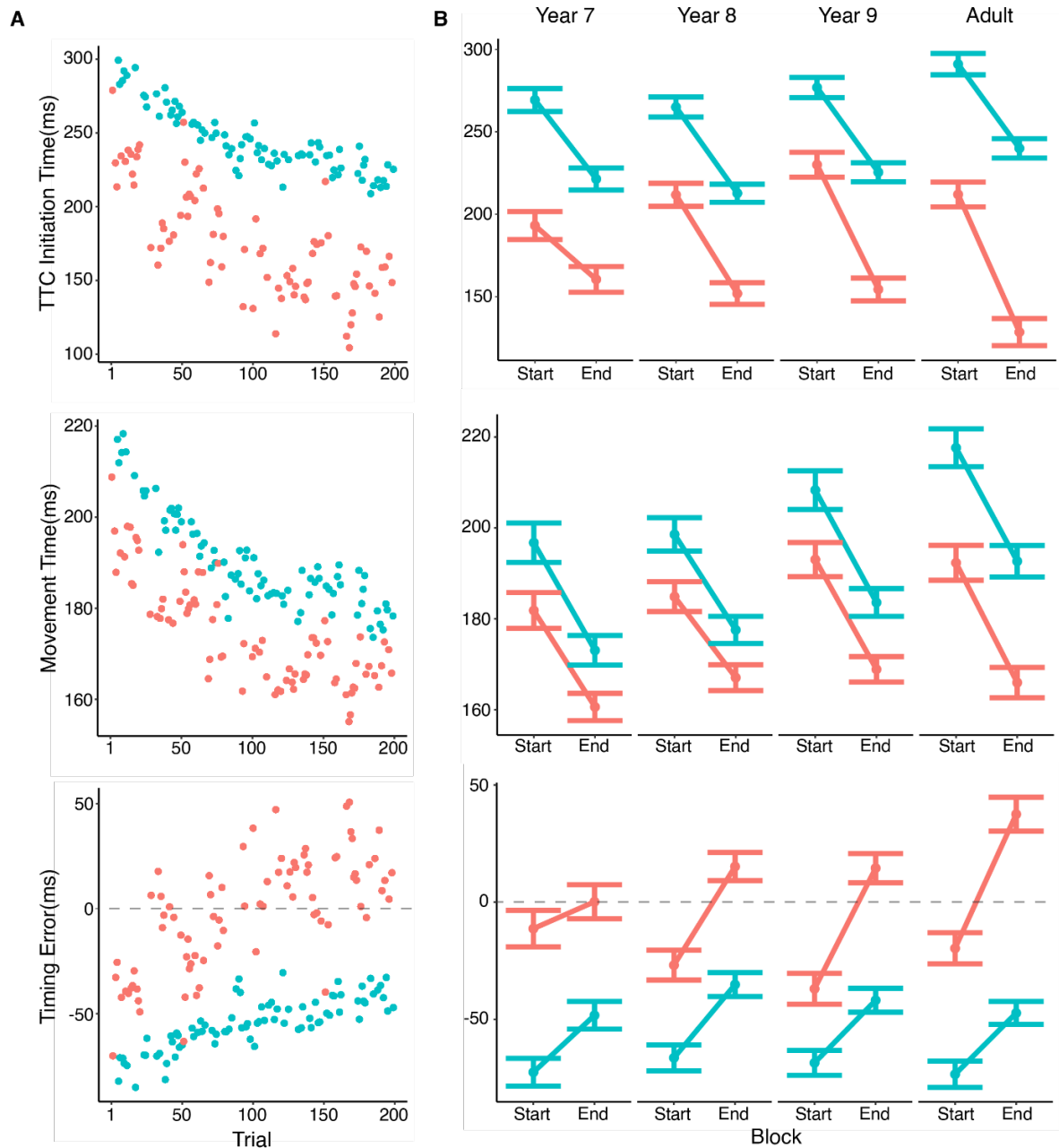


Figure 4.3. Proactive changes to movements across certain and uncertain conditions. A) Summary comparison of trial-by-trial Initiation Times (top), Movement Times (middle), and Timing Errors (bottom), between Certain (blue) and Uncertain (red) conditions. All participants delayed their initiation, shortened their movement times, and arrived later to the target in Uncertain conditions and as the experiment progressed. B) Comparison of differences at the start (i.e. first 50 trials) and end (i.e. final 50 trials) between the different age groups. As participants aged, they delayed initiation and arrival more, in Uncertain, relative to Certain conditions. Dots represent group means with error bars extending to 95% confidence intervals.

Table 4.3. Age-related change models. The results from mixed model ANOVAs examining the effects of Year Group, Certainty, and Time on Initiation Time (top), Movement Time (middle), and Timing Error (bottom).

Initiation Time

Effect	F(df1, df2) =	p
Year Group	(3, 255) = .670	.571
Certainty	(1, 255) = 398.33	< .001***
Time	(1, 255) = 391.64	< .001***
Year Group*Certainty	(3, 255) = 5.80	< .001***
Year Group*Time	(3, 255) = 3.81	.01062*
Certainty*Time	(1, 255) = 9.50	.00228**
Year Group*Certainty*Time	(3, 255) = 6.42	< .001***

Movement Time

Effect	F(df1, df2) =	p
Year Group	(3, 255) = 2.14	.0951
Certainty	(1, 255) = 216.48	< .001***
Time	(1, 255) = 128.05	< .001***
Year Group*Certainty	(3, 255) = 6.63	< .001***
Year Group*Time	(3, 255) = .463	.708
Certainty*Time	(1, 255) = .840	.360
Year Group*Certainty*Time	(3, 255) = .374	.772

Timing Error

Effect	F(df1, df2) =	p
Year Group	(3, 255) = .379	.768
Certainty	(1, 255) = 312.44	< .001***
Time	(1, 255) = 199.27	< .001***
Year Group*Certainty	(3, 255) = 3.66	.01306*
Year Group*Time	(3, 255) = 4.73	.00312**
Certainty*Time	(1, 255) = 13.52	< .001***
Year Group*Certainty*Time	(3, 255) = 6.64	< .001***

Interleaved between each block of *inhibition* trials was a block of 12 *bonus* trials in which the speed of the target was manipulated. This was to provide a range of timing constraints over which we could produce a hitting performance metric without observing ceiling and floor effects (Giles et al., 2018). Typically, later, briefer movements are made in response to

increased timing constraints (i.e. faster targets) which result in less variability in timing error (J. R. Tresilian & Lonergan, 2002; J. R. Tresilian, Plooy, & Carroll, 2004; James R. Tresilian, 2005). Indeed, two-way mixed ANOVAs revealed that adolescents initiated later ($F(3, 603) = 363.27, p < .001$), made briefer movements ($F(3, 603) = 54.85, p < .001$), and acted with more precision ($F(3, 603) = 12.95, p < .001$), in response to faster targets (Fig. 4.3). The only other significant effect was year group on precision ($F(2, 201) = 4.54, p = .0118$), with older participants displaying less variability in their timing errors. There were no significant interaction effects, suggesting all ages adopted this strategy to minimise the variability of their error.

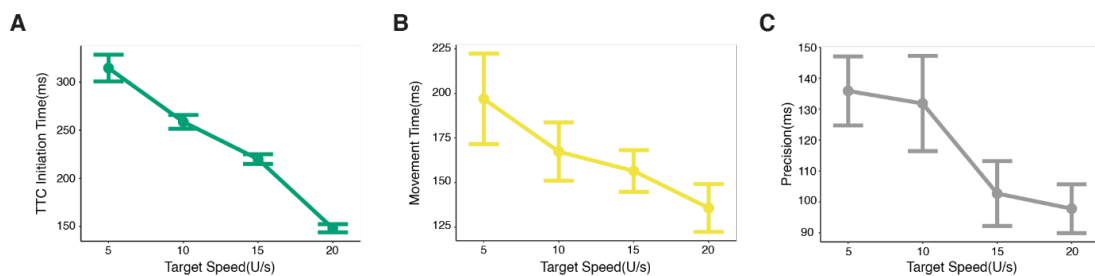


Figure 4.4. Empirical verification of Bonus Block interceptive timing performance. In response to faster targets, participants initiated later (A), moved quicker (B), and reduced the variability of their timing errors (C). This was true for each of years 7, 8, and 9, with no interaction effects. Dots represent the overall group means with error bars extending to 95% confidence intervals.

4.2.2. Reactive inhibition had reached maturity by the onset of adolescence, whereas proactive inhibition was still developing into mid-adolescence

We combined adolescent data with adult data to quantify age-related changes (Fig. 4.5). We found there were improvements to *hitting performance* as participants aged ($F(3, 255) = 9.318, p < .001$). Specifically, adolescents in year 7 ($71.7\% \pm 3.2; p < .001$), year 8 ($71.4\% \pm 2.7; p < .001$), and year 9 ($75.5\% \pm 2.6; p = .0366$), performed significantly worse than adults ($81.2\% \pm 3.0$). There were, however, no age-related changes to *stop-signal reaction times* ($F(3, 255) = 1.020, p = .384$) with year 7 ($207\text{ms} \pm 15.5$), year 8 ($204\text{ms} \pm 14.2$), year 9 ($191\text{ms} \pm 15.5$), and adults ($194\text{ms} \pm 15.8$), performing equally well, suggesting by Year 7, there were no further developmental gains to be had.

Additionally, there were proactive changes to movements as participants aged. For *initiation time* and *timing error*, in addition to main effects of time and certainty (as above), there were interactions at all levels, suggesting as participants got older, they delayed their initiation and arrival more in Uncertain conditions, as the experiment progressed (Table 4.2; Fig 4.3B). *Movement time*, however, only exhibited main effects of time and certainty (as above), with a single interaction between Year Group and Certainty, indicating participants quickened their movements more as they got older, but the magnitude was comparable between age groups across the experiment (Table 4.2; Fig. 4.3B).

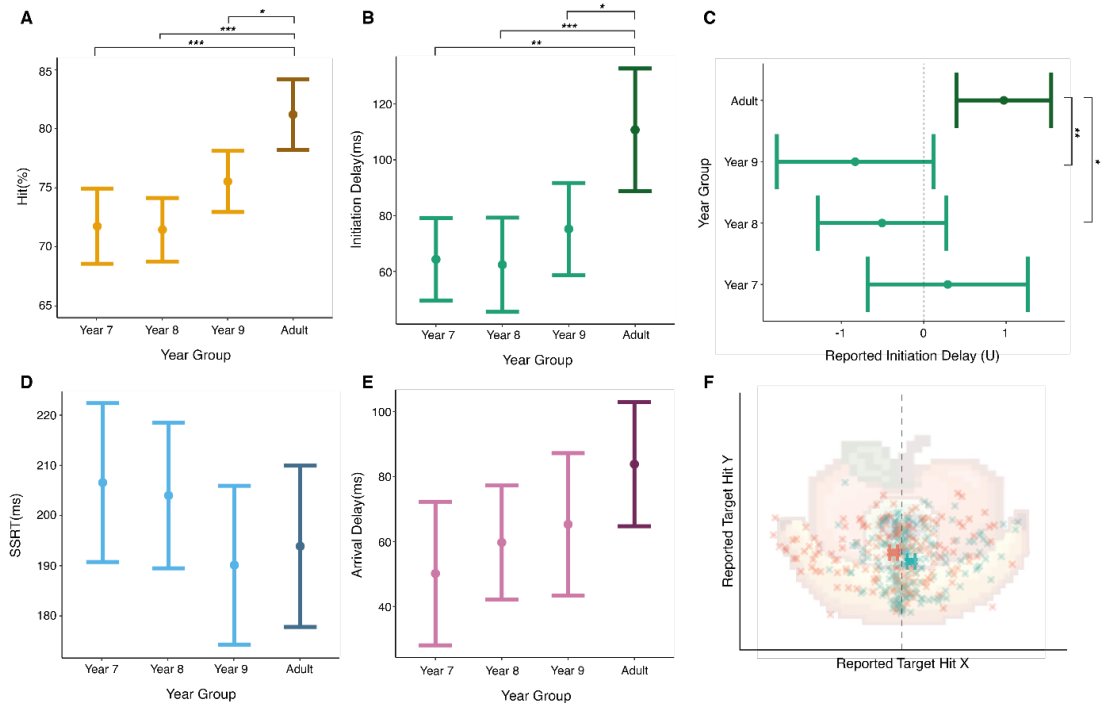


Figure 4.5. Age- related changes to A) Hitting performance, B) Reactive Inhibition, C) Proactive (initiation) delay, D) Proactive (arrival) delay, and E) Reported proactive (initiation) delay. As participants aged, they hit more targets in the bonus blocks (A), delayed initiation more in uncertain trials (C), and reported significantly delayed initiations as Adults (E). There were no age-related changes to reactive inhibition (B) or Proactive (arrival) delay (D). The dots (error bars) are the group means (95% confidence intervals). Significance levels between groups are annotated as follows: * $<.05$; ** $<.01$; *** $<.001$. F) Reported position of where participants aimed to hit the target in each condition (normalized by reported bat position). Each cross represents a single participant, the dots (error bars) are the group means (95% within-subject adjusted CIs). All ages reported aiming significantly further to the back of the target in Uncertain conditions.

We subsequently simplified these comparisons to consider only *initiation delays* and *arrival delays* in the final *inhibition* block. This was because we could directly compare these observed changes in behaviour to the changes in initiation and arrival that were reported at the end of the experiment using our assay. We found there were differences in *initiation delays* ($F(2, 255) = 5.914, p < .001$) between adolescence and adulthood. Participants in year 7 ($64.3\text{ms} \pm 14.8$; $p = .0031$), year 8 ($62.9\text{ms} \pm 16.9$; $p < .001$), and year 9 ($75.2\text{ms} \pm 16.5$; $p = .0324$), delayed initiation significantly

less than adults ($111\text{ms} \pm 22.0$). There were not, however, any changes to *arrival delays* ($F(3, 255) = 1.743$, $p = .159$), with small increases through years 7 ($50.2\text{ms} \pm 22.1$), 8 ($59.7\text{ms} \pm 17.6$), 9 (65.3 ± 21.9), and into adulthood ($83.8\text{ms} \pm 19.1$), proving statistically insignificant.

4.2.3. Participants deliberately aimed further to the rear of the target at all ages, but only adults were explicitly aware of initiation delays

After the experimental blocks had concluded, a self-report assay was run to determine whether proactive changes to movements were governed by explicit processes. Participants indicated where on the screen the target was when they initiated (*target position*), and where on the target and bat they were trying to hit (*target hit*), in both Certain and Uncertain conditions.

A 2 x 4 mixed ANOVA on *target position* revealed no main effect of Year Group ($F(3, 188) = .698$, $p = .554$) nor Certainty ($F(1, 188) = .007$, $p = .930$). There was however an interaction ($F(3, 188) = 4.21$, $p = .00654$), with Adults reporting initiating once the target had moved further ($.973 \text{U} \pm .574$) in Uncertain conditions relative to Certain conditions, which was significantly further than Year 8s ($.505 \pm .781$; $p = .0319$) and Year 9s ($.831 \pm .950$; $p = .00892$) but not Year 7s ($.292 \pm .970$; $p = .669$). Only Adults had non-zero spanning confidence intervals, suggesting only adults were aware of initiating later in the target's trajectory (Fig. 4.5).

A 2 x 4 mixed ANOVA on *target hit* revealed a main effect of Certainty only ($F(1, 188) = 20.29$, $p < .001$) with participants aiming further to the rear of the target in Uncertain ($-.118 \text{U} \pm .059$) compared to Certain conditions ($.151 \text{U} \pm .059$). There were no effects of Year Group ($F(1, 188) = 1.13$, $p =$

.339) nor any interaction ($F(3, 188) = 1.88, p = .134$), suggesting all age groups were explicitly aware of aiming further to the rear of the target when they were unsure if a stop-signal would appear (Fig. 4.5).

4.2.4. *Hitting performance and proactive inhibition independently predicted mathematics attainment*

Finally, we tested whether interceptive timing and inhibition metrics independently predicted mathematics attainment. Standardised attainment scores in mathematics were obtained for each participant from their school. We used z-scores of interceptive timing ability (i.e., *hitting performance*), reactive inhibition (i.e., *SSRT*), and proactive inhibition (i.e., *initiation delay* and *arrival delay*) as predictors in a multi-level model of *maths attainment*, with *school* and *assessment* as random slopes, and *gender* and *year group* as additional controls. The best performing model included fixed effects for *hitting performance* and *arrival delay* (Fig. 4.6):

$$\text{Mathematics}_{ijk} \sim \beta_0 + \beta_{\text{year}}\text{Year}_{ijk} + \beta_{\text{gender}}\text{Gender}_{ijk} + \beta_{\text{hit}}\text{Hit}_{ijk} + \beta_{\text{arrdelay}}\text{ArrDelay}_{ijk} + \beta_{\text{hit}\beta_{\text{arrdelay}}}\text{Hit}_{ijk}\text{ArrDelay}_{ijk} + \alpha_j + \alpha_k$$

More specifically, improvement in *hitting performance* was associated with a significant improvement in *maths attainment* ($\beta_{\text{hit}} = 1.35, t(189.39) = 2.017, p = .0451$). Furthermore, those who *delayed arrival* to the target more also tended to perform significantly better at *mathematics* ($\beta_{\text{arrdelay}} = 1.69, t(187.4) = 2.382, p = .0182$). These effects were independent and there was no interaction between the two ($\beta_{\text{hit}\beta_{\text{arrdelay}}} = .484, t(189.32) = .779, p = .437$).

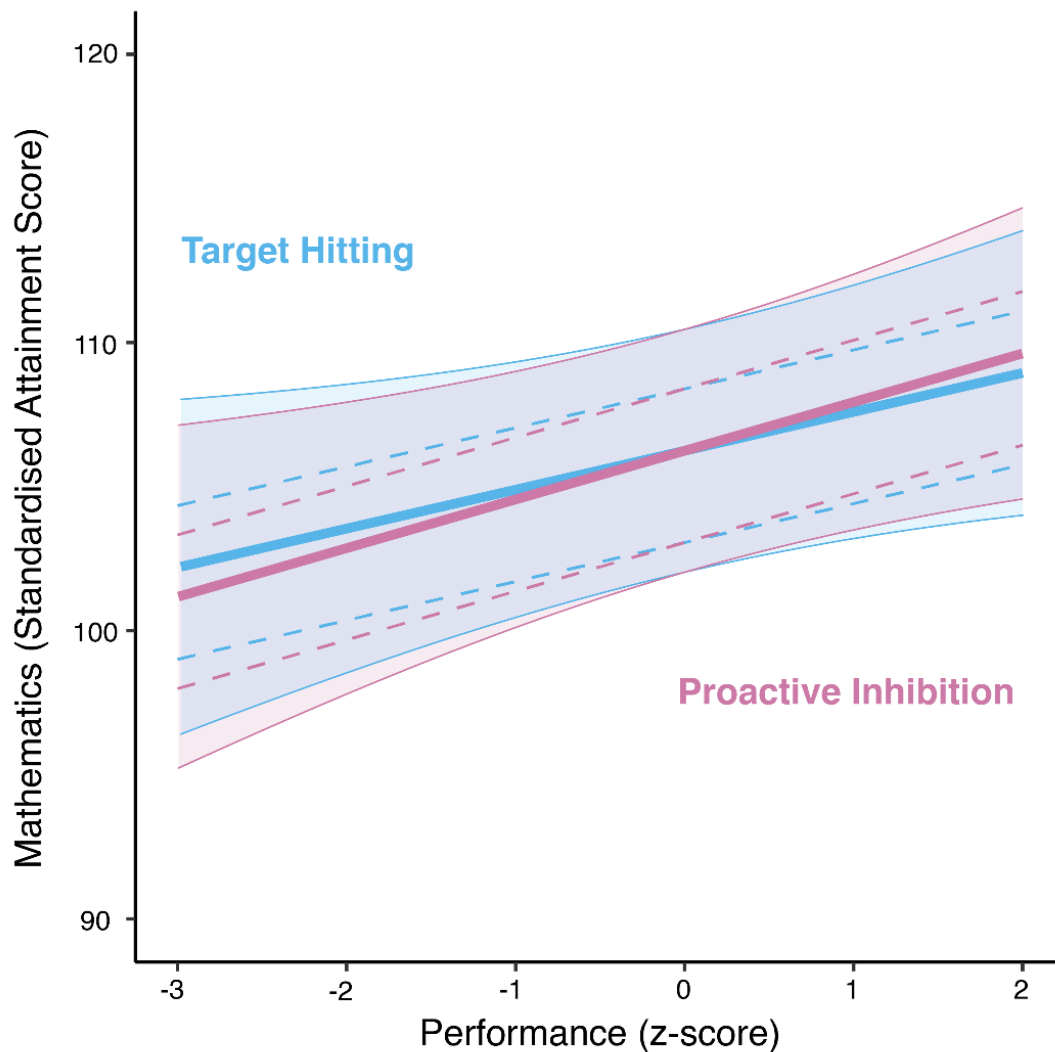


Figure 4.6. Partial plots of the relationships between bonus targets hit percentage (blue) and proactive arrival delays (red), to Mathematics attainment in adolescents. Improvements in proactive inhibition (i.e., greater delays to arrival) were associated with slightly greater increases in Mathematics attainment than equivalent improvements in hitting performance. The solid lines represent the mean estimate, with the shaded area covering 95% confidence intervals. The dashed lines represent the intercepts for the two different standardised assessments that were used. Intercepts for the different schools were effectively zero and are not shown.

Table 4.3. Best performing mathematics attainment model. The percentage of targets hit and proactive delays to arrival independently predicted mathematics attainment. P-values were calculated using Satterthwaite's degrees of freedom method.

Random Effects

Group	Variance	SD
School	.009	.093
Assessment	7.96	2.82
Residual	82.5	9.08

Fixed Effects

Beta	Estimate	df	t	p
Hit	1.350	189.39	2.017	.0451*
Arrival Delay	1.689	187.34	2.382	.0182*
Gender	1.044	189.29	.787	.433
Year Group	-.073	187.88	-.520	.609
Hit*Arrival Delay	.484	189.32	.779	.437

4.3. Discussion

We adapted a novel stop-signal task in which adolescents and adults tried to hit moving targets. This enabled us to produce metrics on *reactive* inhibition, *proactive* inhibition, and interceptive performance, illustrating the course of their development through early adolescence and compared to adulthood. We found it was *proactive* and not *reactive* inhibition that continued to mature through to mid-adolescence. Moreover, we were able to further probe the previously established link between interceptive actions and inhibition, and attainment in mathematics, considering separate *reactive* and *proactive* sub-domains. We found *proactive* inhibition was the dimension of interest, with both target hitting performance and delays to movement timing independently predicting attainment in mathematics.

Firstly, we empirically validated the suitability of the adapted task for use with adolescent populations. Considering whether participants' movements were suitably constrained by manipulating target speed in the *bonus* trials. We found all ages made briefer movements in response to faster targets, which resulted in delayed initiation and less variability in their errors (Fig. 4.4A-C). This is in agreement with stereotypical observations in other studies with adult (J. R. Tresilian & Lonergan, 2002; J. R. Tresilian, Oliver, & Carroll, 2003) and adolescent (Chapter 2) populations. This is thought to be adaptive as increased timing demands require more precision, and is predicted by an open-loop scheme in which movement times are pre-programmed in response to initial estimates of the target's trajectory (James R. Tresilian, 2005).

All assumptions of the independent race model of inhibition were met (Fig. 4.2A-D). Additionally, the mean adolescent stop-signal reaction time ($201\text{ms} \pm 8.60$) aligns with estimates for adults in the original version of this task (Chapter 3) as well as previous estimates in the context of interceptive actions (Marinovic et al., 2009). We also found *proactive* changes to interceptive actions at all ages. Specifically, participants delayed initiation and arrival to the target, while shortening movement times, in response to stop-signal uncertainty. Over the course of the experiment there were greater delays to initiation and arrival whereas the shortening of movement time remained constant (Fig. 4.3). This is also consistent with the findings from Chapter 3.

Subsequently we considered any developmental improvements to *reactive* and *proactive* inhibition in early- to mid-adolescence. In the case of

the former, stop-signal reaction times had reached adult levels by year 7 (ages 11-12; Fig. 4.5D). This replicates previous studies using stop-signal (Dupuis et al., 2019; Ridderinkhof et al., 1999; Williams et al., 1999) and alternative constructs of inhibition (Leon-Carrion et al., 2004; Luna et al., 2004; Tamm et al., 2002) which have found adult levels of inhibition are reached by the age of 12.

We did, however, observe changes to *proactive* inhibition between adolescence and adulthood, with significantly greater delays to the onset of movement in the adult group in anticipation of a stop-signal, compared to adolescents up to age 14 (Fig. 4.5B). Moreover, there were greater proactive delays to initiation and arrival over the course of the experiment as participants aged, whereas there were no age-related changes to differences in movement time over the course of the experiment (Fig. 4.3B).

These findings are of great significance because while the links between PFC maturation and observational changes in self-regulation are well established into the mid-20s, experimental constructs of inhibition previously failed to show any improvements after 12 years of age. For the first time, we demonstrate that measures of *proactive* inhibition should be considered in the normative development of adolescent inhibitory control when considering anything other than the very earliest stages of adolescence.

We hypothesised proactive inhibition would emerge later because only when the limits of reactive inhibition were known, could movement onset be deliberately and maximally delayed, and the target still hit. Our data points

further towards a more nuanced understanding of the processes underlying this maturation. While proactive initiation delays continue to lengthen between year 9 (ages 13-14) and adulthood, proactive delays to target arrival had already reached maturation (Fig. 4.5E). Indeed, this was mirrored by the self-report assays, with participants of all ages reporting aiming further to the rear of the target (Fig. 4.5F), but only adults reporting significant delays to their initiation (Fig. 4.5C) when a stop-signal could appear.

In the case of hitting moving targets, therefore, it would seem proactive inhibition first emerges as an explicit strategy to delay arrival to the target, while implicitly delaying initiation to increase the chances of detecting a stop-signal. Only once the maximum tolerance for late arrival has been reached, do participants deliberately further delay their initiation, compensating with a greater reduction in movement time.

Our interest in experimental constructs of adolescent inhibition is not entirely driven by theoretical gaps in the empirical record. Of course, if they are to be useful, they must also predict real-world outcomes for teenagers. While, previously, we found a broad construct of inhibition predicted mathematics attainment independently from age, gender, and target hitting performance (Chapter 2), here, we found that it was *proactive* and not *reactive* inhibition that is predictive.

Indeed it has been argued that *proactive* inhibition may represent the more ecologically relevant domain of inhibition in clinical contexts, with an addict's substance avoidance, for example, unlikely to recruit reactive mechanisms in response to external stimuli, but rather, the ability to delay

the expression of impulsive behaviours (Aron, 2011). In educational contexts, we hypothesized inhibition would play a role in determining academic outcomes because inhibitory deficiencies are similarly associated with difficulties self-regulating, which often manifests as poor behaviour in class (Jacobson et al., 2011). Adjacent, therefore, our results suggest it is the ability to delay the expression of inappropriate behaviours and responses which have a bearing on attainment, rather than reactive mechanisms. This helps to explain why some recent studies may have failed to find a link between inhibition and attainment (e.g., Donati, Meaburn, & Dumontheil, 2019), because it was *reactive* and not *proactive* domains that were considered.

It should be noted that while *arrival* delay was the mode of proactive inhibition in our best performing maths attainment model, *initiation* delay was also a significant predictor in an alternative model containing the same terms (Table 4.3). Of course, because the arrival delays will be highly correlated with initiation delays when there is little change in movement time, it is unsurprising these models are mutually exclusive, with the best performing model containing only a single domain of *proactive* inhibition. For the sake of completeness, all models we considered containing terms for *reactive* inhibition were not predictive (Table 4.3).

While we have considered inhibition among neurotypical adolescents in an educational setting, these findings may have important clinical implications. Impaired *reactive* inhibition is the principal neurophysiological hallmark of attention deficit hyperactivity disorder (ADHD) (Dimoska, Johnstone, Barry, & Clarke, 2003; Lijffijt, Kenemans, Verbaten, & Van

Engeland, 2005; McAuley, Crosbie, Charach, & Schachar, 2014). Indeed, not only have SSRTs been used to identify children with ADHD (Senderecka, Grabowska, Szewczyk, Gerc, & Chmylak, 2012), there are current attempts to develop treatments for ADHD diagnosed adolescents' based on improving their *reactive* metrics (McKay et al., 2022). Conversely to the present findings, it is deficiencies in *reactive* and not *proactive* inhibition that have been associated with ADHD (Suarez et al., 2021; Van Hulst et al., 2018). Nevertheless, these studies only considered the development of children up to the age of 12.

The present study suggests this may not reflect a genuine absent indication, rather, *proactive* inhibition may not have reached a level of maturation by which deficiencies are manifest between clinical and neurotypical populations. Moreover, there are concerns that purported declines in ADHD symptomatology through adolescence are illusory and, rather, diagnostics are poor at recognising signs of the disorder during this period (Sibley et al., 2012). At the very least, therefore, future research is indicated investigating *reactive* and *proactive* metrics of inhibition in ADHD populations of mid-late adolescents, improving our understanding of the condition, and perhaps also avenues of detection and treatment among these groups.

In summary, an interceptive stop-signal task was used to assess reactive inhibition, proactive inhibition, and interceptive performance, in teenagers and adults. We found that while reactive inhibition had reached maturity by 12 years of age, proactive inhibition continued to show improvements between mid-adolescence and adulthood. This bridges the

empirical gap between symptomatological imaging and experimental studies which characterise adolescence as a period of risk-taking which emerges from imbalances in the PFC and deficiencies in inhibitory control. There is a strong indication, therefore, measures of proactive inhibition must be taken to understand the development of inhibition in adolescent populations. Indeed, such assessments appear to have value in applied educational contexts, with interceptive timing and proactive inhibition independently predicting attainment in mathematics. Whether this utility can extend to clinical populations is an important open question for future research.

4.4. Materials and Methods

4.4.1. Participants

Two-hundred and twenty-three participants from academic years 7 (ages 11-12 years), 8 (ages 12-13 years), and 9 (ages 13-14 years) participated. They were recruited from two state secondary schools in the city of Bradford, UK. Ten participants failed to complete the task in the allotted 30-minute session. Additionally, participants were screened for having completed the inhibition blocks as intended. Specifically, they had to hit more than 80% of targets in each condition, more than 80% of trials had to feature movement times less than 300ms, their probability of responding to a stop-signal must be between 40% and 60%, and the probability of omitting an appropriate go response must be less than 10%. Nine participants were excluded at this stage (5 for hit performance and 4 for elevated probability of stopping), yielding a final

sample of 204 adolescents (100 female; 107 school A; 58 year 8, 80 year 9, 66 year 10).

Sixty-eight adult participants were recruited in addition from Prolific, an online recruitment platform. All participants resided either in the UK or US, had English as their first language, and had a minimum Prolific approval rate 95%. Participants received £3.50 upon successful completion of the study, which took approximately 25 minutes to complete. Pay was contingent on completion and not performance. Four participants were omitted for having more than 5 missing trials. The remaining participants were also screened for performance as above, with eight further participants excluded at this stage (4 for hitting performance, 3 for elevated probability of stopping, and 2 for long movement times). The final sample of adults, therefore, comprised 55 participants (22 Female, $\text{Mean}_{\text{age}} = 30.36$, $\text{SD}_{\text{age}} = 9.05$).

The study was approved by the School of Psychology Ethics Committee at the University of Leeds (Reference: PSYC-116; Date: 27/10/2020).

4.4.2. Experimental Task and Equipment

Participants completed a browser-based game, *Fruit Bat Splat*, in which they had to hit targets moving across a screen with a bat that was controlled by the movement of their mouse. The game was programmed in Unity (ver. 2019.4.4f1) and implemented in WebGL.

School sessions were conducted using school IT facilities. School A provided desktop computers (intel i5 @ 2.3GHz, 8Gb RAM, integrated graphics) and 13" inch displays (1440x900 @ 60/75Hz). School B provided

laptops (Lenovo Thinkpad Chromebook: intel i3 @ 2.30GHz; 4Gb RAM; integrated graphics) with 13.3" displays. Adult participants used their own personal hardware. Frame data were checked for timings and consistency to ensure the task ran at participants' native framerate throughout. All dimensions hereafter are given in Unity units (U) because Unity units scale with the resolution of the screen. A reference resolution of 1920x1080 was used with screen dimensions of 17.75Ux10U with 1U corresponding to 108 pixels. Screens that were not native 16:9 were letterboxed to preserve the dimension of their longest side.

The task is an adapted version of a task previously developed to measure reactive and proactive inhibition in the context of timed interception (Chapter 3). This time, however, an additional task was interleaved between each block to assess target hitting performance at different target speeds. Please refer to chapter 3 for the technical specification of the inhibition elements of the task. Any changes introduced in the current study are detailed below.

4.4.3. Procedure

Prior to the experiment, adult participants indicated whether they were using a mouse or trackpad to control the cursor. Then they calibrated their cursor to ensure movements were approximately equivalent between individuals. Using a sensitivity slider, participants reported when a 5U displacement of the bat corresponded to a "single flick" (mouse) or "single vertical stroke" (trackpad). This mapping was subsequently used throughout the experiment.

Adolescent participants, on the other hand, exclusively used mice to control the cursor. Moreover, because these devices were standardised across the school, the sensitivity was hard coded to the above specification without the need for individuals to calibrate.

The session began with participants being trained to move using ballistic movements to hit the target and to withhold movement in stop-trial conditions (Chapter 3 for details). After participants demonstrated their understanding through a series of practice trials, they proceeded to the experiment proper.

The experiment consisted of 4 *inhibition* blocks interleaved with 4 *bonus* blocks. Each *inhibition* block was further comprised 20 Certain trials and 30 Uncertain trials. In Certain conditions, all trials were go-trials in which it was always safe to hit the target with the bat. Of the Uncertain trials, 20 were go-trials and 10 were stop-trials in which the sun spontaneously rose after the target had begun to move and participants tried to withhold their movements (Fig. 4.1D).

At the end of each *inhibition* block, a confetti animation was displayed for 2s and a “Bonus round” graphic appeared across the screen, signifying the start of a *bonus* block. Each of these blocks comprised 3 trials at 4 different Target Speeds (5, 10, 15, and 20 U/s), with the background replaced for a plain white screen, and the target, bat, and cave stimuli shrunk by factors of 0.67, 0.5, and 0.5 respectively. The cumulative sum of total bonus targets hit was displayed in the bottom left-hand corner of the screen and participants were instructed to hit as many as they could. This combination of Target Speeds and stimuli sizes were determined through

piloting to produce the greatest range of hitting performance over relatively few trials.

The order of stop-trials within Uncertain conditions, Certainty within *inhibition blocks*, and Target Speeds within *bonus blocks* was randomised with all participants experiencing the same order.

Following the main experimental blocks, two assays were included in which participants reported: where on the screen the target was when they tried to initiate; where on the target they tried to hit; and where on the bat they were using to hit the target. The assay was repeated for both Certain and Uncertain condition.

4.4.4. Kinematic Analysis

All analyses were conducted after experimental data had been collected. Firstly, the position time series from each trial was resampled to a standard frequency of 100Hz. This is because Unity samples input at the same frequency as the monitor's refresh rate which varied between schools' and adults' setups. We then filtered the data using a zero-lag, 1st order, low-pass Butterworth filter with 20Hz cutoff. The sample rate and filter were identical to the specification we previously used with this task (Chapter 3).

Interceptive timing metrics were calculated as before (Chapter 3), with the *initiation time* (IT) calculated as the initial time at which the lowermost edge of the bat had crossed the center of the start-zone. Initiation times were then converted to time to contact (TTC) initiation times by subtracting the observed initiation time from 1100ms. The resulting TTC initiation time thus expresses the time prior to the center of the target passing

the interceptive point the initiation is made, with larger values earlier, and smaller values later in the target's trajectory. The *movement time* (MT) was calculated as the time elapsed from the initiation time to the point at which the bat crossed the interceptive plane. We used cubic interpolation on all positions of the center of the target and the center of the bat, from initiation time until max movement amplitude, to estimate the precise moment the bat's center intersected the interceptive plane (i.e., the y-position of the lowermost edge of the target). The *timing error* (TE) was calculated by dividing the displacement between the centers of the target and bat and dividing by the speed. Positive timing errors indicate the center of the bat arrived later than the center of the target, negative timing errors earlier.

Three 4 x 3 mixed ANOVAs were run on each of *initiation time*, *movement time*, and the standard deviation of *timing error*(precision), with year group as the between groups factor and target speed as the within groups factor. This was to confirm canonical observations that briefer movements should be made in response to faster target speeds, resulting in greater precision (i.e., decreased standard deviation of timing error), and that this was age invariant. Prior to this analysis all trials where *movement time* or *timing error* exceeded 1 second were removed (647/9629 = 6.7% trials) to ensure we considered only those trials in which movements were reasonably constrained. All ANOVAs were type III to account for the fact the year groups comprised unbalanced numbers. Contrasts were set to ensure they summed to 0. Where sphericity was violated, effects are only reported when Greenhouse-Geisser corrections were also significant at the $p < .05$ level.

4.4.5. Stop-signal Reaction Times

Stop-signal Reaction Times (SSRTs) were estimated from Uncertain trials in the *inhibition* blocks only. They were calculated for each participant using the integration method. Initiation times on go-trials were ranked and the n th trial was found where n is the total number of go-trials multiplied by the probability of responding. Individuals' mean stop-signal delays (SSD) were subtracted from their go-trial initiation times on the n th trial to find their SSRT. This is suitable when using a staircasing procedure with at least 40 stop trials and their incidence is 33% or less (Matzke, Verbruggen, & Gordon, 2020). Trials on which go responses were incorrectly omitted were assigned the maximum initiation time observed (Verbruggen et al., 2019). Trials were then ranked according to their initiation time. The n th IT was selected where n is the probability of responding given a stop-signal multiplied by the number of go responses observed. The SSRT was found by subtracting the mean stop-signal delay from the n th IT (Matzke et al., 2020). Actual values of the SSD were used to compute the mean (cf. programmed values) as the precise presentation of the stop-signal depended on the refresh rate of the display (Verbruggen et al., 2019). Summary statistics of the variables used to calculate SSRTs are displayed in Table 4.1.

4.4.6. Proactive Inhibition

Differences in *initiation time*, *movement time*, and *timing error*, on go-trials between Certain and Uncertain conditions represent our measures of proactive inhibition. Additionally, when considering the effects of proactive inhibition, we wanted to ensure participants were timing their initiations to

move with ballistic movements. Accordingly, trials were removed in which participants initiated before the target had crossed the halfway point, after the target had left the screen, or with a movement time of more than 300ms. In total, 4124/40750 (~10.1%) trials were removed at this stage.

The mean of each measure for each participant over the first 50 (start) and final 50 (end) trials were taken as our measures of proactive inhibition at both the start and end of the experiment. The group means (95%CI) are presented in figure 4.3B. All data are reported as mean $\pm$ 95%CI across all subjects.

Firstly, we performed two-way repeated measures ANOVAs on IT, MT, and TE, considering the effects of certainty (2 levels: Certain; Uncertain), and time (2 levels: Start; End) using adolescent data only. This was to check adolescents made proactive changes to their movements. We subsequently added the adult data and performed mixed model ANOVAs to determine the significance of the effects of proactive control (i.e., certainty) over the course of the experiment (i.e., time) on each dependent variable between the different age groups (4 levels: Year 7; Year 8; Year 9; Adult). The results can be seen in table 4.2.

4.4.7. Age related changes

Adolescent and adult data was combined. Separate one-way independent ANOVAs were run on the percentage of targets *hit* in the *bonus* block, *stop signal reaction time*, *proactive initiation delay*, and *proactive arrival delay*, with year group (4 levels: year 7; year 8; year 9; and adult) as the independent factor. We simplified proactive comparisons to consider only

initiation delays and *arrival delays* in the final *inhibition* block, by computing mean difference scores in *initiation time* and *timing error* between Certainty conditions for each participant over final 50 *inhibition* trials. This was because we could directly compare these observed changes in behaviour to the changes in aim that were reported at the end of the experiment using our assay.

All ANOVAs were type III to account for unbalanced groups. Tukey's post-hoc tests were performed where a significant effect was found to determine the levels at which the differences were significant. All data are reported as mean $\pm$ 95%CI across all groups.

4.4.8. Reported Aim

We had two explicit measures of proactive control in each condition. *Reported target position* is how far the target had travelled when participants reported they tried to initiate their movement in each condition. *Reported target hit* is where on the target participants reported aiming to hit the target in each condition. The latter was centred by subtracting away the point of the bat they reported using to hit the target. One adult and 26 adolescent participants were omitted from this stage of analysis (failed to provide any data). Additionally, 3 adults and 38 adolescents were removed for reporting the target had moved less than 1.5U before initiating. Accordingly, 192 participants were considered in total.

2 x 4 mixed-model ANOVAs were run with Certainty as the within groups factor and Year Group as the between groups factor to determine whether participants were actively aware of adjusting their initiation or arrival

in response to uncertainty, and whether there were any age-related differences. Difference scores between Certainty conditions for each participant were also calculated which are displayed at the year group level in figure 4.4D. All data are reported as mean $\pm$ 95%CI across all groups.

4.4.9. Attainment Scores

Standardised attainment scores were obtained from both schools for each consented participant. In years 7 and 8, these comprised scaled scores from MidYis assessments that were sat when pupils first entered year 7. Maths attainment scores were taken directly from the Maths sub-score of the MidYis assessment. MidYis scores are scaled to produce a normal distribution with a mean of 100 and standard deviation of 15. Participants in year 9 did not sit MidYis assessments at school entry thus attainment scores were taken from performance in KS2 SATs. SATs are standardised tests taken across the UK at the end of primary school in year 6. The scaled score from the Maths SAT were taken as maths attainment. SATs scores are scaled to produce a normal distribution with a mean of 100 and a standard deviation of 10.

4.4.10. Attainment Models

Prior to modelling, 12 students were removed for missing attainment data with 193 participants included in the final analysis.

Linear mixed effects models were constructed to predict maths attainment. Participant age was grouped by academic year group and centered around the median year such that it ranged from -1 to 1 with single unit increments. We then converted proportion of targets hit (hitting performance), stop signal reaction time (reactive inhibition), initiation delay (proactive inhibition 1), and arrival delay (proactive inhibition 2) into z-scores (mean = 0, sd = 1). This was to ensure all parameter estimates were directly comparable. In all our models, gender and year group were included as additive terms to control for the fact older males tended to perform better in the task, and school (A or B) and assessment (MidYis or SATs) were included as random intercepts to account for the fact that mean attainment scores might vary between these distinct populations.

Our modelling was based on previous work which reported relationships between hitting performance, inhibition, and academic attainment (Chapter 2). Nevertheless, because we had no principled reason to prefer one domain of inhibition over the other, we first considered a model containing hitting performance, reactive inhibition, and proactive inhibition, with interaction terms. We then considered separate models for reactive inhibition, and each measure of proactive inhibition, combined with hitting performance. We then computed the best fitting, most-parsimonious model using likelihood ratio tests (Winter, 2013). The best performing model was

then compared to a null model containing only year group, gender, and random intercepts for school and assessment.

All statistical analysis was conducted in *R*(v4.2,1). Linear mixed effect models were fit using maximum likelihood estimation implemented in the *lme4*(v1.1-29) package. P-values were obtained for each parameter via Satterthwaite's degrees of freedom method as implemented in the *lmerTest* (v3.1-3) package.

4.5. References

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Chapter 5: Discussion

For millennia, the survival of our species has hinged on our ability to intercept moving targets. Whether catching prey or deflecting an advancing attack, our success has relied not only on the planning and execution of an accurately timed movement, but also on the ability to inhibit that movement in response to information emerging later in the target's trajectory. In the modern day, elite batters push the biological limits of our capabilities in the game of baseball. Equally, however, the ability to intercept moving targets may have wider developmental significance among the general population, providing neurodevelopmental markers for use in educational and clinical contexts.

The link between sensorimotor skills and mathematics has long been documented, but the underlying mechanisms are a matter of debate. On the one hand, it may emerge from a neural architecture common between spatiotemporal and mathematical operations. Alternatively, it may be incidental to shared control processes overseeing the two. The preceding chapters have sought to resolve this controversy. In doing so, several ancillary questions have also been addressed. Using kinematic data, it's been possible to shed new light on our understanding of the mechanisms underpinning proactive inhibition. Additionally, the developmental trajectories of interceptive timing and reactive and proactive domains of inhibition have been detailed through to mid-adolescence, providing novel insights into the ontogeny of these aspects of behaviour critical to progressing successfully into adulthood.

5.1. Summary of Experimental Chapters

In the first experimental chapter (Chapter 2), *de novo* adolescent data was combined with data previously obtained with primary school children (Giles et al., 2018) using a 1-df interceptive timing task. Plotting the developmental trajectory of interceptive performance revealed that up to the age of 15, adolescents had yet to reach adult levels. Participants at all ages seemed to exploit the fact that faster movements yield more accurate temporal estimates under increased timing constraints (James R. Tresilian, 2005). Developmental performance gains, therefore, must be attributed to some alternative (or combination of) mechanism(s). The measure of inhibition derived from the kinematic data may give some clue. Younger participants, for example, made more “false-starts”, and this too showed improvement into adulthood. This is consistent with the hypothesis that developmental improvements to interceptive performance might be attributed to concurrent improvements in inhibitory control observed throughout childhood and adolescence.

Central to the present thesis, however, was the finding interceptive performance and the putative measure of inhibition independently predicted attainment in mathematics. This favours the “shared processing” hypothesis (e.g. Anderson, 2010) because only one of these predictors would have reached significance in the statistical models if the variance shared between attainment and interceptive timing was the same variance that was shared with inhibition. Therefore, rather than the link being explained in terms of shared executive control processes overseeing the two (e.g. Hulme, 2019), the first experiment suggests distinct mechanisms contributed.

To rigorously interrogate the relationship, however, *bona fide* measures of inhibition in the context of interceptive actions were required. Recent studies have shown inhibition can be further decomposed into *reactive* and *proactive* components (Aron, 2011). Rather than appropriate the original interceptive stop-signal task (Marinovic, Plooy, & Tresilian, 2009), therefore, a novel 1-df interception task was developed that could measure stop-signal reaction times, and additionally permitted comparisons between movements in conditions where stop-signals could and couldn't appear as measures of *proactive* inhibition. Not only would this task have to be highly scalable to assess participants in their hundreds, but it would also have to be deliverable remotely to circumvent the considerable restrictions imposed by the covid-19 pandemic. Accordingly, a browser-based version of the task was developed in Unity and hosted using Amazon Web Services, in which participants controlled the bat using their mouse or trackpad.

In Chapter 3, an adult population was recruited to empirically validate the task. The results showed that the assumptions of the independent race model of inhibition were met, permitting the valid calculation of stop-signal reaction times. Reassuringly, these values aligned with those previously reported using a 1-df stop-signal task (Marinovic et al., 2009). This also indicated that participants were suitably constrained on trials where a stop signal might appear that comparisons between kinematics on trials where stop signals would never appear could yield measures of proactive inhibition. Indeed, under the uncertainty of whether a stop-signal would appear, participants delayed initiation and arrival to the target, which was accompanied by a shortening of movement time,

While proactive movement delays have previously been observed using simple button press tasks (e.g. Verbruggen & Logan, 2009; Zandbelt et al., 2013), this is the first time proactive changes to movement planning have been observed downstream initiation. Interestingly, the shortening of the movement time was not sufficient to preserve the arrival time (i.e., timing error), with targets struck further to the rear in uncertain conditions.

Assuming interceptive movement times are programmed in advance (James R. Tresilian, 2005), this suggests both response suppression and “waiting” strategies contributed to proactive delays. The shortening of the movement time represented how much longer participants waited prior to the go-process being triggered, whereas arrival delays reflected increases to the completion threshold for go-processes that had already been triggered. Moreover, for the first time, the extent participants were aware of proactive delays was probed using a spatial assay. While delays to both initiation and arrival were reported, observed delays were greater, challenging the notion proactive inhibition is driven entirely by explicitly retrievable processes.

Finally, in Chapter 4 the task was adapted to additionally incorporate an assessment of interceptive performance over a range of target speeds. This permitted parametric assessment of interceptive timing, and *reactive* and *proactive* domains of inhibition. Returning to the central question of this thesis, interceptive performance and *proactive* (but not *reactive*) inhibition independently predicted mathematics attainment in adolescents. Including both *reactive* and *proactive* measures of inhibition as predictors, this comprehensively demonstrated that any relationship between interceptive timing and mathematics is governed by mechanisms distinct from those

shared with inhibitory control (c.f., Hulme, 2019). This favours a “shared processing” account in which the relationship emerges from a common neural architecture supporting both sensorimotor and mathematical operations (e.g., Anderson, 2010).

Further analyses were also permitted with the inclusion of an adult population. Once again, there was a gulf in interceptive performance between adults and teenagers, confirming interceptive performance does not reach maturity by mid-adolescence. Moreover, while it was confirmed *reactive* inhibition had fully developed by the onset of adolescence (e.g., Dupuis et al., 2019), there were still *proactive* gains to be made, with adults delaying initiation significantly longer than the eldest teenagers included in the sample (~14 years old). Perhaps, therefore, the protracted development of interceptive timing performance observed in Chapter 2 and Chapter 4, can at least in part be attributed to improvements in the capacity to maximally delay timed interceptive actions, thus ensuring they are initiated when, and only when, appropriate.

Finally, the relative immaturity of *proactive* inhibition in mid-adolescence has important implications for applied research. While adolescence is commonly characterized as a period of impulsivity and recklessness, hitherto experimental measures of inhibition had not aligned with this narrative. The present thesis suggests that to adequately capture normative development of inhibition in adolescents, however, measures of *proactive* inhibition must be included. Adjacently, in the case of mathematics, at least, *proactive* inhibition seems to be the sole domain of inhibition that has any bearing on real-life educational outcomes.

5.2. Limitations and Future Directions

There are several notable constraints to the research in the present thesis.

Firstly, limitations to the central question concerning the nature of the link between interceptive timing and mathematics will be considered.

Subsequently, a discussion of the limitations surrounding *proactive* inhibition and adolescent development will follow. In both cases, avenues and recommendations for future research are highlighted.

Shared processing and neural reuse have profound implications in applied settings. According to this view, neural circuits established for one purpose (e.g., spatiotemporal estimates) can be repurposed for other functions (e.g., mathematical operations) (e.g., Anderson, 2010; Andres, Michaux, & Pesenti, 2012; Anobile et al, 2020). One advantage of this framework is that it can explain how cognitive abilities such as mathematics can emerge, despite being too recent in our phylogenetic history for specialized circuits to have been established through evolution (Dehaene, 2004). Put simply, they must be learned, and this occurs through the shaping and assignment of existing structures through ontogenetic development (e.g., Dehaene, 2004, Pulvermuller, 2018). This implies that functional relationships exist between these processes. Under this view, therefore, the ability to perform mathematical operations is a direct consequence of sensorimotor interactions through development. Not only does this predict that sensorimotor skills will correlate with mathematics attainment, but also that training in sensorimotor skills could yield like for like improvements in mathematics. This is obviously attractive to educators. Firstly, such assessments promise to provide valuable insight into the challenges

students face when learning mathematics. Secondly, and more radically, there's the potential for additional avenues of intervention when traditional pedagogical approaches fail.

While the current thesis provides evidence in favour of shared processing, it is not possible through cross-sectional studies, such as the ones contained here, to establish causation. A priority for future research, therefore, would be to establish a causal link between interceptive performance and mathematics. Firstly, longitudinal studies including parametric measures of interceptive timing and executive function would enable more sophisticated modelling techniques capable of probing the causal structure of these links. Secondly, a randomized control trial is indicated in which an intervention designed to improve interceptive abilities can be deployed to determine the effects on mathematics attainment. It should be noted that similar trials have recently been undertaken with mixed results (e.g., Asakawa et al., 2019, Erasmus et al., 2016). These trials have taken a very general view of sensorimotor skills, however, and were not targeted to a domain as specific as interceptive timing which places a premium on the accuracy of spatiotemporal estimates, and thus the very foundations upon which mathematical operations are theorized to rest. Indeed, brief perceptual training in numerosity tasks have brought improvements to children's symbolic arithmetic skills (Hyde, Khanum, & Spelke, 2014). Given that numerosity is implicated in representations of time and space (Anobile, Arrighi, Castaldi, & Burr, 2020), it is not so farfetched that interceptive training might similarly improve arithmetic.

Another considerable limitation of the present study is the lack of other measures of executive control contained within the analyses. Thus, while there is certainty the relationship between interceptive performance and mathematics is not entirely accounted for by inhibitory control processes shared between the two, perhaps the control processes of *updating* and *shifting* would account for the remaining variance. It should be noted that this is unlikely, inhibition is highly correlated with *updating* and *shifting*, perhaps even indistinguishable (Miyake & Friedman, 2012). Indeed, it is thought that *updating*, which includes the maintenance of task relevant goals in working memory, is a necessary component of the *proactive* control processes examined in the present thesis (Chevalier, James, Wiebe, Nelson, & Espy, 2014). Similarly, any role for attentional shifting might have been captured as an interaction between interceptive performance and inhibition, whereby rapid online corrections must be made if movements are initiated inappropriately early. This was observed in the case of English attainment in Chapter 2 where interceptive performance was only predictive of attainment in those who were poor inhibitors. Nevertheless, future studies also including parametric measures of *updating* and *shifting* are indicated to unequivocally demonstrate that interceptive timing and mathematics are linked by mechanisms distinct from common control processes overseeing the two.

Finally, with respect to the central question, there were a couple of limitations imposed by the reality of conducting research during the covid-19 pandemic and in applied settings. Firstly, it was not possible to access University facilities to validate measures of SSRT in a laboratory setting with a suitable control task. Thus, while every effort was made to empirically

validate the novel task, a more rigorous protocol is required to assess the concurrent validity of it with pre-existing measures of SSRT. Secondly, measures of mathematics and English ability were provided by the school in the form of standardized attainment scores. This introduced two difficulties for analysis. Firstly, they were not always directly comparable because of changes introduced to the national curriculum between the year groups considered. Moreover, these only form general indications of a child's or teenager's ability in the respective discipline. Equivalent measures of specific sub-domains which directly assessed the hypothesized links (i.e., arithmetic), may have produced more precise models with greater effect sizes, and should be pursued in future studies if possible.

Scrutinizing the shared processing hypothesis was the focus of the preceding experimental chapters. In doing so, several auxiliary findings were made that contribute to our understanding of inhibition. Perhaps the most significant contribution was observing proactive changes to movements downstream from initiation, with participants delaying their arrival to the target. It should be emphasized that this is not entailed by delayed initiation, in other contexts (e.g., target speed increases) initiation delays are accompanied by proportional reductions in movement time to preserve timing error (J. R. Tresilian, Oliver, & Carroll, 2003). The present findings indicate, therefore, proactive inhibition was achieved, at least to some extent, by aiming further to the rear of the target. Self-reports of intended strategies revealed this resulted from a combination of explicit and implicit processes.

Nevertheless, it is unclear how generalizable these findings are. The target speed was relatively slow and the target width relatively wide. These

relaxed timing constraints gave a large margin of error to use as a buffer for greater initiation and arrival delays. Ideal for measuring metrics of *proactive* inhibition, but not exactly the challenge faced by elite batters in professional baseball. At this opposite end of the spectrum, such margins are so fine it seems unlikely that it would be possible to meaningfully delay initiation or arrival and still hit the ball. Clearly there is a balance to be struck between two competing goals: hitting the ball and avoiding strikes. By manipulating target speed under stop-signal uncertainty, insights can be made into how individuals balance these goals in the general case.

Similarly, while changes in proactive inhibition were observed over the course of the experiment, with greater delays to initiation and arrival, what it is that drives this behaviour remains an open question. It is well documented that post-hoc sensory feedback about performance is critical to reducing interceptive timing errors (e.g., E. Brenner & Smeets, 2011; de la Malla, Lopez-Moliner, & Brenner, 2012; Scott & Gray, 2010). Proactive response delays likewise appear to be driven by feedback, with greater delays following stop trials (Bissett & Logan, 2011). Thus, timing errors and the incidence of stop trials on preceding trials may act as a suitable starting point from which a computational model of the present data can be built, formalizing how executive processes adjust interceptive movements to balance competing goals.

Claims about the extent to which proactive changes are volitional must also be made with caution. There are issues inherent in the use of self-reported aiming assays. Most notably, they cannot distinguish between whether the behavior was guided by intentional processes, or simply an

insight that was developed when asked about it afterwards (Maresch, Mudrik, & Donchin, 2021). In response to this, a self-report assay was conducted prior to any experimental trials (unpublished). However, this strongly biased participants towards greater delays in initiation and arrival at the onset of the experiment. It seems simply demonstrating that it was possible to initiate later and aim further to the rear, the convergence on proactive strategies was accelerated. And while this observation supports the view that it is indeed possible to volitionally control proactive strategies, that is not to say they are volitionally controlled in the absence of such measures. Much like estimating the position of an electron, it seems that the measurement process changes the measurement itself. Attributing the reported element of the observed behaviour to explicit or implicit processes, therefore, may simply reflect how it has been measured, rather than the processes underlying it (Hadjiosif & Krakauer, 2021).

The present thesis finally contributed to our understanding of adolescent development. There was coincidental evidence in favour of improvements to inhibition (specifically proactive inhibition) yielding improvements in interceptive performance, with both improving through mid-adolescence to adulthood. Once again, however, the cross-sectional nature of the study precludes favoring this explanation over alternatives. For example, improvements to interceptive timing performance may equally have yielded improvements to inhibition, though it's less clear how this mechanism would operate. After all, inhibiting movement until necessary is a pre-requisite for successful interception, whereas being able to successfully intercept targets is not a pre-requisite for successful inhibition. As a

generalized process that is a sub-component of successful interception, it makes more sense for the direction of causation to be from inhibition to interception.

Still, recent research has shown that the relationship between sensorimotor skills and executive functions is complex, with executive functions making a greater contribution to sensorimotor performance in childhood and early adolescence than in adulthood, suggesting at some point in adolescence they begin to develop independently (Gordon-Murer, Stöckel, Sera, & Hughes, 2021). Once again, a longitudinal study is indicated to confirm whether inhibitory gains through adolescence are manifest in coinciding improvements to interceptive performance.

The implications of proactive inhibition showing development through mid-adolescence extends much further than interceptive timing, however. Future observational studies linking proactive inhibition to recklessness and risk-taking may bridge the gap between experimental, symptomatological and brain imaging studies, yielding an important clinical marker that may help to mitigate against the unfortunate consequences of this behaviour through the identification of at-risk individuals.

Further studies are also indicated with clinical populations. It is possible that proactive inhibition may not have reached levels of maturity at the population level capable of discriminating those with deficiencies. While speculative, there is a desperate need to improve diagnostics and understanding of ADHD in mid-adolescence because observed improvements in symptomatology at this age may simply reflect shortcomings of the test, with many continuing to experience difficulties

without recognition or help (Sibley et al., 2012). Indeed, it is troubling that inhibitory deficits in ADHD have only been characterized until the onset of adolescence (Suarez et al., 2021; Van Hulst et al., 2018). By deploying the measures developed in this thesis on studies of adolescents with ADHD, it will be possible to improve our understanding of the symptomatology among these populations, potentially improving identification and outcomes among those whose needs are currently not recognised nor met.

5.3. Conclusion

This thesis has examined the complex relationships between the ability to manually intercept moving targets, inhibitory control, and attainment in mathematics. The development of a parametric assessment of interceptive timing and inhibition has permitted the establishment of a degree of independence between these relationships which may help educators more accurately characterise the difficulties individual children and teenagers face when learning mathematics and, in future, yield novel avenues for intervention. In doing so, new insights have been gained into *proactive* inhibition and its developmental significance through adolescence. These findings are important because they close the gap between health and education. There is increasing evidence to suggest that many children and young people experience health barriers that prevent educational attainment. In turn, poor educational attainment is a major risk factor for poor long term physical and mental health. The novel measures reported in this thesis are deployable at a large scale and could help inform discussions around

connecting health and education services to better provide for the needs of young people in future.

5.4. References

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