

Being Alone

Social Disconnection in Adolescence



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Declaration

This thesis is the result of my own work and includes nothing which is the outcome of work done in collaboration except as declared in the preface and specified in the text. It is not substantially the same as any work that has already been submitted, or is being concurrently submitted, for any degree, diploma or other qualification at the University of Cambridge or any other University or similar institution except as declared in the preface and specified in the text. It does not exceed the prescribed word limit for the relevant Degree Committee.

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Abstract

Social isolation and loneliness are increasingly prevalent worldwide, with individuals aged 16-24 years reporting particularly high levels. This vulnerability during a sensitive window of social and emotional development is concerning given that loneliness strongly predicts mental and physical health outcomes. Despite being one of the loneliest age groups, adolescents report higher social media use than any other demographic. However, the relationship between digital social interactions and loneliness is unclear. While digital social interactions might displace some face-to-face communication, they can also strengthen existing relationships and foster new connections. This thesis investigates social isolation and digital social connection in adolescents, and is divided into two parts.

Part one employs an experimental paradigm to examine the effects of short-term social isolation on human adolescents aged 16-19 years. Using a within-participant design, adolescents underwent baseline testing and sessions of complete isolation and isolation with digital social interactions. Chapter two investigates the effects of social isolation on psychological state and on threat learning. Chapter three investigates the effects of social isolation on reward responsiveness — including reward seeking and reward learning — integrating computational models of learning. Chapter four leverages ultra-high field 7-Tesla MRI to identify neural predictors of sensitivity to isolation.

Part two uses non-experimental methods: chapter five systematically reviews adolescent online and offline self-disclosure, examining whether and how digital social connections fulfil social needs; chapter six examines late adolescents' digital social interactions and loneliness amid social distancing during COVID-19; and chapter seven explores emotional experiences and mental health changes in young people facing social disconnection.

The findings advance our understanding of how social isolation impacts adolescent mental health, bridging human and animal research while highlighting both opportunities and limitations of digital social connections. This work has implications for supporting healthy development and reducing adolescent loneliness in an increasingly online world.

I dedicate this thesis to the friends I made along the way.

*I am no stranger to loneliness. At sixteen, I moved alone across the coast.
At twenty-six, across the country. And at twenty-eight, across the world.*

*Here in Cambridge, I found joy, love and belonging — and I have never felt less alone.
These social connections are my proudest accomplishment and the greatest gift from my PhD.*

I will cherish these times, memories and friendships forever.

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Towner, E., Thomas, K., Tomova, L., & Blakemore, S.-J. (2024). Increased threat learning after social isolation in human adolescents. *Royal Society Open Science*, 11(11), 240101. DOI: 10.1098/rsos.240101

Tomova, L., Towner, E., Thomas, K., Zhang, L., Palminteri, S., & Blakemore, S.-J. (2025). Acute isolation is associated with increased reward seeking and reward learning in human adolescents. *Communications Psychology*, 3(1), 135. DOI: 10.1038/s44271-025-00306-6

¹I would like to express my sincere thanks to all my collaborators. While this thesis is written using the first person singular, "I" should be understood to acknowledge the collective efforts and contributions of my research team.

Contribution

As this thesis was undertaken within the context of collaborative projects, my individual contribution to each chapter is listed below using the Contributor Role Taxonomy (CRediT) system.

1. **General Introduction:** conceptualisation, writing (original draft), writing (review and editing)
2. **The Effects of Social Isolation on Adolescent Threat Learning:** conceptualisation, data curation, formal analysis, investigation, methodology, project administration, software, visualisation, writing (original draft), writing (review and editing)
3. **The Effects of Social Isolation on Adolescent Reward Responsiveness:** conceptualisation, formal analysis, investigation, methodology, project administration, software, writing (original draft), writing (review and editing)
4. **Neural Predictors of Sensitivity to Social Isolation in Adolescents:** conceptualisation, investigation, project administration, writing (original draft), writing (review and editing)
5. **The Role of Online and Offline Self-Disclosure for Social Connection:** formal analysis, methodology, project administration, writing (original draft), writing (review and editing)
6. **Loneliness and Digital Social Interactions during COVID-19:** conceptualisation, data curation, formal analysis, methodology, project administration, visualisation, writing (original draft), writing (review and editing)
7. **The Fear of Missing Out during COVID-19:** conceptualisation, formal analysis, methodology, project administration, supervision, visualisation, writing (original draft), writing (review and editing)
8. **General Discussion:** conceptualisation, writing (original draft), writing (review and editing)

Table of contents

List of figures	xx
List of tables	xxii
1 General Introduction	2
1.1 Social Disconnection	2
1.1.1 The Prevalence of Social Disconnection	3
1.1.1.1 Objective Social Isolation	3
1.1.1.2 Subjective Feelings of Loneliness	4
1.1.2 The Perils of Social Disconnection	5
1.2 Adolescence	5
1.2.1 Social Disconnection Among Adolescents	6
1.3 Adolescence as a Sensitive Period	7
1.3.1 What is a Sensitive Period?	7
1.3.2 Sensitive Periods from a Mechanistic Perspective	9
1.3.3 Is Adolescence a Sensitive Period for Social Isolation?	10
1.3.4 Investigating Sensitive Periods	12
1.3.5 Adolescence as a Window of Opportunity	13
1.4 The Adolescent Brain	13
1.4.1 Biological Bases of Brain Development	14
1.4.1.1 Neuroplasticity During Adolescence	15
1.4.2 Structural Brain Development	17
1.4.3 Brain Function in Adolescence	21
1.4.3.1 Socio-Affective System	21
1.4.3.2 The Social Brain	22
1.4.3.3 Cognitive Control System	22
1.4.3.4 Theories of Adolescent Neurodevelopment	23
1.5 Learning During Adolescence	25

1.5.1	Classical Conditioning – Pavlovian Learning	25
1.5.1.1	Reward Learning	26
1.5.1.2	Threat Learning	27
1.5.2	Operant Conditioning – Instrumental Learning	28
1.6	Adolescent Mental Health	32
1.6.1	Underlying Learning Processes	32
1.7	Adolescents and Social Media	34
1.8	Thesis Overview	37
2	The Effects of Social Isolation on Adolescent Threat Learning	41
2.1	Introduction	41
2.1.1	Aims	43
2.2	Methods	43
2.2.1	Study Design	43
2.2.2	Participants	43
2.2.3	Procedures	45
2.2.3.1	Social Isolation	45
2.2.4	Measures	47
2.2.4.1	Questionnaires	47
2.2.4.2	Threat Learning Task	48
2.2.4.3	Other Tasks	50
2.2.5	Data Analysis	51
2.2.5.1	Psychological State	51
2.2.5.2	Threat Learning	52
2.2.5.3	Mechanisms	53
2.3	Results	54
2.3.1	Psychological State	54
2.3.1.1	Hourly Trends	55
2.3.2	Threat Learning	56
2.3.3	Mechanisms	59
2.4	Discussion	61
3	The Effects of Social Isolation on Adolescent Reward Responsiveness	65
3.1	Introduction	65
3.1.1	Aims	68
3.2	Methods	68
3.2.1	Measures	68

3.2.1.1	Questionnaires	68
3.2.1.2	Effort-Based Decision Making Task	70
3.2.1.3	Reinforcement Learning Task	71
3.2.2	Data Analysis	72
3.2.2.1	Reward Seeking	72
3.2.2.2	Reward Learning	72
3.2.2.3	Mechanisms	77
3.2.2.4	Software	78
3.3	Results	79
3.3.1	Reward Seeking	79
3.3.2	Reward Learning	80
3.3.2.1	Performance	80
3.3.2.2	Computational Modelling	80
3.3.3	Mechanisms	83
3.3.3.1	Reward Seeking	83
3.3.3.2	Reward Learning	84
3.4	Discussion	85
4	Neural Predictors of Sensitivity to Social Isolation in Adolescents	89
4.1	Introduction	89
4.1.1	Aims	91
4.2	Methods	91
4.2.1	Procedures	91
4.2.1.1	Neuroimaging	91
4.2.2	Measures	92
4.2.2.1	Monetary Incentive Delay Task	92
4.2.3	Data Analysis	92
4.2.3.1	Neural Reward Sensitivity	92
4.3	Results	96
4.3.1	Neural Reward Sensitivity	96
4.4	Discussion	97
5	The Role of Online and Offline Self-Disclosure for Social Connection	101
5.1	Introduction	101
5.2	Methods	102
5.2.1	Procedure	102
5.2.1.1	Search Strategy and Inclusion Criteria	102

5.2.1.2	Data Extraction and Analysis	103
5.2.1.3	Quality Assessment	103
5.3	Results	116
5.3.1	Relationship Building	116
5.3.2	Online versus Offline	117
5.3.3	Moderators	117
5.4	Discussion	119
6	Loneliness and Digital Social Interactions during COVID-19	122
6.1	Introduction	122
6.2	Methods	124
6.2.1	Participants	124
6.2.2	Procedure	124
6.2.3	Measures	125
6.2.3.1	Questionnaires	125
6.2.4	Hypotheses	127
6.2.5	Data Analysis	127
6.2.5.1	Post Pandemic Changes	127
6.2.5.2	Pre Pandemic Comparisons	128
6.2.5.3	Loneliness, Depression and Happiness	128
6.2.6	Other	128
6.3	Results	129
6.3.1	Post Pandemic Changes	129
6.3.2	Pre Pandemic Comparisons	130
6.3.3	Loneliness	131
6.3.4	Depression	132
6.3.5	Happiness	133
6.4	Discussion	133
7	The Fear of Missing Out during COVID-19	137
7.1	Introduction	137
7.1.1	The Current Study	138
7.2	Methods	139
7.2.1	Measures	139
7.2.1.1	Qualitative Measure	139
7.2.1.2	Quantitative Measures	139
7.2.2	Data Analysis	140

7.2.2.1	Emotional Experiences	140
7.2.2.2	Emotional Experiences and Changes in Mental Health . . .	141
7.3	Results	143
7.3.1	Emotional Experiences	143
7.3.1.1	Lost Opportunities	144
7.3.1.2	Gained Opportunities	144
7.3.1.3	Loneliness	145
7.3.1.4	Gratitude	145
7.3.1.5	Social Support	146
7.3.1.6	Negative Thoughts	146
7.3.1.7	Self-Reflection	147
7.3.2	Emotional Experiences and Changes in Mental Health	147
7.4	Discussion	148
8	General Discussion	154
8.1	Summary of Results	154
8.2	Considerations	160
8.2.1	Theoretical Considerations	160
8.2.2	Methodological Limitations	162
8.3	Future Directions	164
8.3.1	Social Isolation in the Brain	165
8.3.2	Digital Fulfilment of Social Needs	166
8.3.3	Social Media	167
8.4	Concluding Remarks	168
	References	171
	Appendix*	

*In place of an appendix, supporting materials are available in an online supplement (DOI: 10.17605/osf.io/34j9m).

List of figures

1.1	Adolescence as a Sensitive Window	13
1.2	Cellular Stages of Brain Development	15
1.3	Structural Brain Maturation	19
1.4	Diffusion Tensor Imaging (DTI)	20
1.5	Maturational Imbalance Theory	24
1.6	Emotion Circuitry Reorganisation	25
2.1	Social Isolation Study Design	46
2.2	Threat Learning Task	48
2.3	Psychological State	55
2.4	Psychological State - Hourly	57
2.5	Threat Learning – Arousal Ratings	58
2.6	Threat Learning – Valence Ratings	59
2.7	Threat Learning – Electrodermal Activity	60
2.8	Mechanisms	61
3.1	Reward Responsiveness Tasks	69
3.2	Reward Learning Task – Design Matrix	74
3.3	Reward Learning Task – Optimal Parameters	78
3.4	Reward Seeking – Social Context	79
3.5	Reward Learning – Performance	81
3.6	Reward Learning – Computational Modelling	83
3.7	Mechanisms – Reward Seeking	84
3.8	Mechanisms – Reward Learning from Negative Feedback	85
4.1	Neural Reward Sensitivity	97
6.1	Pandemic Related Changes	130
6.2	Pandemic Related Changes in Primary Practice	131

6.3	Pandemic Related Changes in Household Composition	132
7.1	Depressive Symptoms and Gained Opportunities	149
7.2	Mental Health and Gained Opportunities	150

List of tables

3.1	Reward Learning Model Comparison	82
5.1	Self-Disclosure – Study Summary	104
6.1	Digital Social Interactions – Loneliness	133
6.2	Digital Social Interactions – Depression	134
6.3	Digital Social Interactions – Happiness	134
7.1	Thematic Codebook – COVID-19 Experiences	141

Introduction

Chapter 1

General Introduction

The content of this chapter draws in part from published work:

Towner, E., Chierchia, G., & Blakemore, S.-J. (2023). Sensitivity and specificity in affective and social learning in adolescence. *Trends in Cognitive Sciences*, 27(7), 642–655. DOI:10.1016/j.tics.2023.04.002

1.1 Social Disconnection

Social disconnection is a growing global concern. Both social isolation and loneliness have shown significant increases in prevalence in recent years (Barreto et al., 2021; Buecker et al., 2021; Jeste et al., 2020; Victor and Yang, 2012). In response to this trend, the United States (U.S.) Surgeon General has recently designated loneliness as an epidemic of comparable severity to tobacco use and obesity (Office of the Surgeon General, 2023). Concurrently, the World Health Organization (WHO) has classified loneliness as an urgent global health threat, establishing an international commission dedicated to addressing this issue. Beginning in 2020, the COVID-19 pandemic further intensified this challenge, as social isolation and feelings of loneliness escalated across diverse geographic locations and demographic groups (Ernst et al., 2022).

Across social species, connection to a group enhances survival by reducing risk and conserving energy, adaptations beneficial for survival and optimal functioning (Holt-Lunstad and Sine, 2024). Therefore, social connection can be considered an "innate need" (Baumeister and Leary, 1995; Cacioppo et al., 2014). Interestingly, however, in humans objective isolation and subjective loneliness are related, yet distinct, constructs in that feelings of loneliness can be high even when surrounded by others and, conversely, time spent alone does not always lead to loneliness (Cacioppo and Hawkley, 2009; Leigh-Hunt et al., 2017). Social

isolation, or the objective state of being alone, is characterised by limited social relationships, minimal social roles, few group memberships and infrequent social interactions. Conversely, loneliness manifests as a subjective internal state—a distressing experience that emerges from perceived isolation or differences between an individual's preferred and actual social experience. Loneliness may emerge when our social interactions fail to satisfy our interpersonal needs, arising from a discrepancy in the balance between the desired and actual levels of social connection. Past research has also made a distinction between state loneliness (sometimes called transient loneliness) and trait loneliness (sometimes called chronic loneliness). State loneliness refers to momentary feeling of loneliness, which can fluctuate in daily life and might be more influenced by immediate social contexts and company (Larson, 1990; van Roekel et al., 2014, 2018). Trait loneliness, on the other hand, is defined as a persist experience. Researchers have conceptualised the maintenance of balance between one's actual and desired social connections as the biological process of "social homeostasis". Similar to other homeostatic systems in the body, social homeostasis is proposed to involve mechanisms that help sustain optimal levels of social connection. Feelings of loneliness might function as a signal in the social homeostasis system, similar to hunger or thirst, indicating an unmet need for social connection and thus activating neurobiological and physiological mechanisms that motivate individuals to reconnect (Holt-Lunstad and Sine, 2024).

Therefore, an individual's level of social connection depends on more than just their number of close relationships. Social connection is a multidimensional construct encompassing structural, functional and qualitative components of social relationships (Holt-Lunstad et al., 2017). The structural dimension involves the quantity, diversity (e.g., co-workers, friends, family, neighbours) and interaction frequency within one's social network. The functional dimension addresses how reliably these social connections meet various needs, such as mentorship or emotional support. The qualitative dimension reflects the extent to which these relationships provide positive, supportive and satisfying experiences, rather than negative, unhelpful or dissatisfying ones—for instance, feelings of inclusion versus exclusion within specific social groups. Importantly, social connection exists on a continuum rather than as a dichotomous construct and is inherently dynamic; both its quantity and quality fluctuate over time and might be enhanced or diminished due to various factors.

1.1.1 The Prevalence of Social Disconnection

1.1.1.1 Objective Social Isolation

In recent decades, data from the U.S. have shown reductions in social contact, participation in groups and organisations, community involvement and companionship (Holt-Lunstad and

Sine, 2024; Office of the Surgeon General, 2023). For example, measures of objective social contact from 2003 – 2020 reveal increasing social isolation, with average daily time spent alone rising from 285 minutes (2003) to 309 minutes (2019) and 333 minutes (2020; Kannan and Veazie, 2023). In-person social interactions have steadily declined across relationship types, with time spent with friends decreasing from 60 minutes daily in 2003 to just 20 minutes in 2020 (Kannan and Veazie, 2023). Pandemic-related lockdowns caused a spike in alone time, but, contrary to expectations, Americans spent even more time alone in 2023 than during the height of the pandemic in 2021 (Thompson, 2025).

This trend extends beyond the U.S. Analysis of Time Use Surveys from the United Kingdom's (U.K.) Office for National Statistics and the European Social Survey indicates that young adults are spending more time alone compared to a decade ago (Burn-Murdoch, 2025). In the U.K., the proportion of people living alone doubled between 1990 – 2009 (Ruston, 2003) and has continued to rise. By 2023, 8.4 million people in the U.K. lived alone, representing an 8% increase (620,000 additional individuals) compared with 2013 (Office for National Statistics, 2024). Furthermore, U.K. evidence demonstrates a persistent shift from team sports towards individual activities, despite substantial public investment in organised sports programmes (Harris et al., 2017). Similarly, a review of 25 studies in China documented significant increases in isolation between 1995 and 2011, correlating with rising urbanisation, divorce rates, unemployment and social inequality (Yan et al., 2014).

1.1.1.2 Subjective Feelings of Loneliness

With rising levels of objective social isolation it is perhaps unsurprising that subjective feelings of loneliness have also drastically risen worldwide. Data indicates that roughly one in four individuals—representing 24% of the global population and exceeding one billion people—report feeling either "very lonely" or "fairly lonely" (Gallup Inc. and Meta, 2022). Recent reports suggest that loneliness affects approximately 50% of the adult population in the U.S. (Office of the Surgeon General, 2023). A 2022 study revealed that only 39% of U.S. adults reported feeling strongly connected to others emotionally (Gallup Inc. and Meta, 2022). As of 2022 in the U.K. nearly half of adults (49.63%, 25.99 million people) reported experiencing loneliness at varying frequencies. Chronic loneliness – defined as feeling lonely "often or always" – affected approximately 7.1% of Great Britain's population (3.83 million), an increase from 6% (3.24 million) in 2020, suggesting persistent elevation beyond pre-pandemic levels. Importantly, this is not only a phenomenon in the Global North. In a recent survey, loneliness affected at least a third of the population in 29 countries (Gallup Inc. and Meta, 2022). Of these, 22 were located in Africa, four in the Middle East and three in South Asia, despite perceptions of high social connectedness in these regions.

1.1.2 The Perils of Social Disconnection

Evidence consistently demonstrates that greater social connectedness is associated with increased longevity (Holt-Lunstad et al., 2015). In contrast, loneliness is correlated with elevated risk for heart disease and stroke (Valtorta et al., 2016), substance abuse and premature mortality (Hosseinbor et al., 2014; Leigh-Hunt et al., 2017; Wang et al., 2017). Inadequate social connection might increase susceptibility to viruses and respiratory illnesses (Cohen, 2021). Furthermore, deficient social connection can elevate mortality risk to a degree comparable with smoking up to 15 cigarettes daily (Holt-Lunstad et al., 2017).

In addition to these physical concerns, social disconnection is associated with a host of negative psychological outcomes including depression and anxiety. It has been proposed that social disconnection underlies the current co-occurring "crises" of both loneliness and mental health decline (Holt-Lunstad and Sine, 2024). A systematic review of longitudinal studies revealed that adults who frequently experience loneliness have more than double the odds of developing depression compared to those who rarely or never feel lonely (Mann et al., 2022). Moreover, evidence consistently identifies social isolation as potentially the strongest and most reliable predictor of suicidal ideation, attempts and completed suicide across demographically diverse populations varying in age, nationality and clinical severity (Van Orden et al., 2010). Therefore, loneliness extends far beyond mere emotional discomfort. It poses a significant threat to both individual wellbeing and public health at the societal level. Social disconnection might present elevated risk during certain stages of development such as adolescence – a unique period of heightened affective and social sensitivity (Towner et al., 2023).

1.2 Adolescence

Adolescence is defined as the period of life beginning with the onset of puberty and culminating with the establishment of a stable, independent adult role (generally conceptualised as the ages between 10 to 24 years; Sawyer et al., 2018). Adolescents have long been described as being emotional and particularly interested in peer relationships. Over 2000 years ago Aristotle described youth as "passionate, irascible and apt to be carried away by their impulses ... the age when people are most devoted to their friends".

Adolescence was first recognised as a distinct stage of development worthy of scientific study beginning in the early twentieth century by psychologist Stanley Hall (Hall, 1904). He coined the term "storm and stress" to describe adolescence, viewing it as a period of heightened emotional turmoil and behavioural challenges. Contemporary research has revealed that there are indeed marked changes in affect in adolescence. Compared to adults, adolescents report

emotions that are more frequent, intense and volatile (Guyer et al., 2016). Studies demonstrate that adolescents (aged 14 – 18 years) report feeling both more euphoric and more depressed in response to events over the course of a typical week, and their positive emotions did not last as long as those of adults (Guyer et al., 2016; Larson et al., 1980). Adolescent emotions tend to be more complex and nuanced than those of children (Burnett et al., 2011) and self-conscious social emotions such as embarrassment, shame and pride peak in adolescence (Somerville et al., 2013). Compared to adults, adolescents are particularly reactive to both positive and negative affective valence, and display, for example, both increased reward pursuit (Marshall et al., 2020) and threat avoidance in some contexts (Blakemore, 2018; Klein et al., 2021). Adolescents also show greater behavioural sensitivity to both appetitive and aversive stimuli (Galván and McGlennen, 2013).

Adolescence is also thought of as a period of social reorientation in which social connections become increasingly important (Tomova et al., 2021; van den Bos, 2013). As adolescents progressively become independent from their caregivers and find their place amongst peers, the social world becomes increasingly salient. For example, adolescents found pleasant social photographs more rewarding to look at than pleasant non-social (nature) photographs, and the reverse was true for adults (Andrews et al., 2019). Studies have shown that self-reported "desire to be liked" peaks in late adolescence (approximately age 21 years) (Altikulaç et al., 2019) and that social rewards are subjectively more attractive than monetary rewards for children and adolescents, compared to adults (Ethridge and Weinberg, 2018). Social threats also become more salient in adolescence. Being rejected by peers in an online chatroom paradigm resulted in enhanced pupil dilation (a response elicited by emotional intensity) in adolescents aged 9 – 17 years, and this effect was stronger in older adolescents than in those in the younger age range (Silk et al., 2012). Further, heightened emotionality in adolescence is most often and most strongly experienced in social settings (Guyer et al., 2016).

1.2.1 Social Disconnection Among Adolescents

Social disconnection has become a critical issue for adolescents today (Buecker et al., 2021; Twenge et al., 2021). Worldwide reports on chronic loneliness indicate that adolescents rank among the age groups most affected (Hammond et al., 2019; Twenge et al., 2021, 2019), although findings demonstrate some heterogeneity (Mund et al., 2020). Surveys indicate that loneliness levels are particularly high among 16 – 24-year-olds, surpassing all other age groups in many countries (Barreto et al., 2021). Further, global rates of loneliness among adolescents aged 13 – 18 have increased significantly since around 2012, predating the COVID-19 pandemic, with sharper rises observed amongst girls (Twenge et al., 2021, 2019). Shifting trends in social contact have been most pronounced in adolescents. According to U.S. data,

declines in social contact are most stark among young people aged 15 – 24 (Kannan and Veazie, 2023), with this demographic experiencing a nearly 70% reduction in time spent in-person with friends over almost two decades, decreasing from approximately 150 minutes per day in 2003 to 40 minutes per day in 2020. Adolescents today demonstrate markedly different social behaviours compared to previous generations. They are obtaining driver's licences at lower rates, engaging in fewer romantic relationships, maintaining smaller friendship circles and participating in less frequent in-person socialisation (Thompson, 2025). The proportion of adolescents who report daily social interactions with peers outside of educational settings has decreased by approximately 50% since the early 1990s, with the most significant reduction occurring during the 2010s (Thompson, 2025). U.K. and European data also demonstrate that social disconnection has reached its highest levels among teenagers and young adults in recent decades. Data from the European Social Survey reveals that the proportion of young people who socialise less than weekly has risen from 10% to 25% (Burn-Murdoch, 2025). Considering the increased emotional volatility and the central role of social connections during adolescence, the growing issue of social disconnection warrants significant concern. Adolescents might be particularly vulnerable to isolation-induced loneliness and its consequent detrimental outcomes, as adolescence might represent a *sensitive period* of development.

1.3 Adolescence as a Sensitive Period

1.3.1 What is a Sensitive Period?

According to Bornstein's (1989) conceptual framework, a sensitive period is a window of time during which experience exerts an especially pronounced impact on development. Before or beyond this window, development in that domain may still occur but is typically less efficient or less robust. In contrast, a critical period denotes a strictly bounded window within which specific experiences *must* occur to achieve typical development. Criteria for functional evidence of sensitive periods involves revealing an outsized and lasting impact of a particular input on a particular outcome during a discrete period. Importantly, the terms "sensitive period" and "period of heightened sensitivity" require careful differentiation. While both phenomena are scientifically valuable and worthy of investigation, they are distinct. Periods of heightened sensitivity refer to instances where certain stimuli evoke greater attention and affective reactivity without necessarily¹ resulting in changes that are specific, outsized and long-lasting – essential prerequisites for classification as a sensitive period.

¹Though in some contexts long-term changes (i.e., learning) certainly could be enhanced by heightened sensitivity (discussed further in Section 1.5)

Numerous developmental processes in humans and animals appear to exhibit sensitive or critical periods that often—though not invariably—manifest in very early life. Seminal research by Hubel and Wiesel (1965), using an animal model, demonstrated that if visual input to one eye is disrupted during early life, normal binocular vision fails to develop. Further, remediation outside a specific early window often cannot fully restore typical functioning. These findings have been replicated in humans in studies of infants with congenital cataracts (that block visual inputs). Surgical treatment to remove the cataracts before six weeks of age has been shown to provide optimal rehabilitation of visual acuity (Birch and Stager, 1996).

Beyond sensory domains, some facets of more complex, *psychosocial* functioning show evidence of sensitive periods. Strong translational evidence points to infancy as a sensitive period for attachment formation to a caregiver. A classic example is avian imprinting. Imprinting only occurs within a very brief window after hatching, during which the chick learns to identify its mother and initiates a following response for proximity (Hess and Schaeffer, 1959; Lorenz, 1935; Upton and Sullivan, 2010). Birds possess a biological drive for proximity seeking, but this limited sensitive period is the crucial time when the animal learns *who* the object of its attachment will be. More recent research in animal models has demonstrated rigorous evidence of a sensitive period for attachment learning. For example, infant rodents readily learn odours, facilitating the acquisition of their mother's scent and motivating them to approach their caregiver. This drive to approach persists even when the odour is associated with painful stimuli (see Callaghan et al., 2019; Upton and Sullivan, 2010 for reviews). In humans, there is also evidence that infancy might be a sensitive period for a toddler to form a secure attachment with their caregiver. In an experimental study it was found that toddlers (aged 42 months) randomly assigned to foster care exhibited a greater likelihood of demonstrating a secure attachment relationships with their caregivers compared to toddlers who remained in institutional care (Smyke et al., 2010). Importantly, these effects were age-specific. Only children placed in foster care in their first two years of life (before 24 months of age) showed this effect. Responsive caregiving, specifically during infancy, appears important for children to develop a secure attachment relationship.

The evidence on attachment suggests that sensitive periods are not limited to sensory functions but also extend to facets of psychosocial development. Yet, this research still focuses on sensitive periods occurring very early in life. This prompts consideration regarding whether all sensitive periods end within the first few years of life. Contrary to this assumption, evidence indicates that some sensitive periods might be protracted, starting later and enduring for a longer duration. It has long been posited that there is a sensitive period for second language learning (Lenneberg et al., 1967). Research on second-language acquisition shows that learners who begin second language study before approximately 12 years of age can more easily achieve

native proficiency (Johnson and Newport, 1989). Although second language learning remains *possible* beyond this age, it tends to be considerably more difficult (though more recent research using computational modelling on a dataset of over 600,000 participants suggests that this sensitive period extends to age 17.4 years before declining steadily; Hartshorne et al., 2018).

Given the evidence for sensitive periods in complex functions (such as psychosocial development) and those with protracted timing (such as second language learning), it is plausible that sensitive periods for late-emerging higher cognitive abilities might exist during adolescence. For example, adolescence has been suggested as a potential sensitive period for emotion regulation (Gee, 2016; Silvers, 2022; Woodard and Pollak, 2020) and sociocultural processing (Blakemore and Mills, 2014). However, it is important to note that complex and multifaceted functions (particularly in humans) are likely to manifest as a series of multiple, overlapping sensitive periods for specific processes rather than a single sensitive period for broad constructs like social and emotional development (Cheng et al., 2024; Gabard-Durnam and McLaughlin, 2020; Hensch and Bilimoria, 2012).

1.3.2 Sensitive Periods from a Mechanistic Perspective

While the *functional* evidence discussed above focuses on outcomes (e.g. vision, attachment, second language learning, etc.) neuroscientists have often focused on a more *mechanistic* perspective regarding sensitive periods, defining and identifying sensitive periods based on underlying neurobiology². From this perspective, sensitive periods are developmental learning mechanisms that neurobiologically encode particular, expectable environmental experiences (Gabard-Durnam and McLaughlin, 2020). For example, in the seminal work by Hubel and Wiesel (1965), it was changes to the visual cortex of the brain (not to the eyes themselves) that mediated functional changes in vision. Mechanistically, therefore, sensitive periods are characterised by the underlying neurobiological processes that govern heightened neuroplasticity during specific developmental windows (Gabard-Durnam and McLaughlin, 2020). Indeed, functional evidence alone might be insufficient to identify sensitive periods from this theoretical perspective. The mechanistic perspective suggests that evidence of sensitive periods must, by definition, demonstrate underlying neuroplasticity that includes substantial, rapid changes to brain function, involves the tuning of neural responsiveness to specific environmental inputs, occurs only during specific windows of development for specific brain circuits and is consolidated by factors that actively repress neuroplasticity to protect the experience-modified circuitry and produce enduring effects on brain function and behaviour (Gabard-Durnam and McLaughlin, 2020). The cellular mechanisms underlying heightened periods of neuroplasticity

²This type of research is often complementary to functional perspectives.

and their measurement are further discussed in Section 1.4. In both human and animal models, research has shown functional and mechanistic evidence suggestive of adolescent sensitive periods in various domains (Blakemore and Mills, 2014; Cheng et al., 2024; Fuhrmann et al., 2015; Gerhard et al., 2021; Luciana and Collins, 2022; Schalbetter et al., 2022). Below, I will focus specifically on whether adolescence represents a sensitive period for the effects of social isolation.

1.3.3 Is Adolescence a Sensitive Period for Social Isolation?

Animal research has documented unique effects of social deprivation, including complete social isolation, on brain and behavioural development during adolescence. These animal models typically involve depriving animals of any social contact with their own species and studying resulting changes both during and after social isolation. Isolation in adolescent rodents, even for a brief period (e.g., 24 hours), can trigger behavioural changes such as heightened anxiety (Maisonnette et al., 1993), hyperactivity (Morley and Worsham, 1978), and increased sensitivity to social rewards (Ikemoto and Panksepp, 1992). This heightened sensitivity can also extend to the pursuit of food or drug rewards, making these animals more susceptible to addiction (McCool and Chappell, 2009). Consistent with the results from rodent studies, anxiety-like behaviours are also seen in adolescent non-human primates after 1 – 3 weeks of peer deprivation (Cinini et al., 2014). While reintroducing isolated animals to social interaction can mitigate some short-term effects, such as anxiety (Maisonnette et al., 1993), certain long-term consequences, including increased ethanol consumption, persist even after social reintegration (Wolffgramm and Heyne, 1991). Chronic isolation during adolescence produces even more profound effects. Rodents isolated throughout adolescence exhibit abnormal behaviours, including hyper-reactivity to stress (Heidbreder et al., 2000) and heightened aggression (St Popova and Petkov, 1990). Additionally, isolation negatively impacts cognitive processes (such as attention and memory) and reduces cognitive flexibility, leading to impaired performance in related tasks (Amitai et al., 2014; Robbins, 2016; Schrijver and Würbel, 2001). Studies have also examined the effects of social deprivation during peak social play periods (Vanderschuren and Trezza, 2013), instead of complete isolation throughout adolescence. These studies typically isolate animals from their peers from around postnatal days 21 to 43, roughly equivalent to early adolescence (aged 10 – 13 years) and mid-adolescence (aged 14 – 16 years) in humans (Burke et al., 2017). Results of studies that isolate animals only during peak social play periods are similar to those that investigate isolation throughout adolescence. These studies show increased anxiety-like behaviours, depression-like behaviours, and reward-seeking (Novick et al., 2018). Additionally, increased aggression is observed when rodents are raised with genetically modified conspecifics that display reduced social interaction

(Stark and Pellis, 2020), suggesting that behavioural changes can also occur under less severe forms of social deprivation.

Social isolation during adolescence has been found to cause significant structural and functional changes in the brain in animal models. These changes are particularly prevalent in the dopamine and serotonin neuromodulatory systems, especially within brain regions important for functions involving reward, memory and cognitive control. Following adolescent isolation in rodents, dopamine release in the nucleus accumbens (a reward region) increases, while dopamine activity in the prefrontal cortex (a cognitive control region) decreases (Hall, 1998; Lukkes et al., 2009b; Novick et al., 2018). Additionally, serotonin levels are also affected, with the direction of the effects varying between brain regions. For instance, the prefrontal cortex exhibits increased serotonergic activity, whereas other areas, such as the hippocampus (a brain region involved in learning and memory), display decreased activity. These alterations are believed to underlie behavioural changes such as increased anxiety and hyperactivity (Burke et al., 2017; Hall, 1998). Even in cases where rodents are not entirely isolated but are deprived of peer contact by being raised solely with an adult animal, brain-level changes are observed, including reduced synaptic pruning in the prefrontal cortex (Bell et al., 2010). In non-human primates, deprivation of contact with peers for 1 – 3 weeks results in a reduction in cell proliferation and neurogenesis in the hippocampus (Cinini et al., 2014). It is important to note that these effects are specific to isolation during adolescence and are not as pronounced when isolation occurs before or after this developmental stage (Hall, 1998; Novick et al., 2018).

Very little research has investigated the effects of adolescent social isolation in humans. However, the COVID-19 pandemic offered an interesting "natural experiment" in which in-person social interactions were drastically reduced. A rapid systematic review (Loades et al., 2020), conducted early in the pandemic, examined the relationship between loneliness and mental health problems in healthy children and adolescents. The review also investigated whether previous disease containment measures (such as those implemented during H1N1 and SARS outbreaks), including quarantine and social isolation, predicted future mental health problems. Results indicated that social isolation and loneliness increased the risk of depression, and possibly anxiety, both at the time of measurement and during follow-up periods ranging from 0.25 to 9 years later. Notably, the duration of loneliness demonstrated a stronger correlation with mental health symptoms than did the intensity of loneliness. Similarly, COVID-19 lockdowns, which resulted in school closures, have been linked to mental health issues among students who experienced prolonged physical isolation from peers, teachers, extended family and community networks (Loades et al., 2020; Makinodan et al., 2012; Xiong et al., 2022). Separately, a study comparing adolescent mental health before and after school closures due to the COVID-19 pandemic found that depressive symptoms increased during this

time, rising from 18.5% before schools closed to 24.9% just after they reopened (Zhang et al., 2020b). This emerging evidence suggests that social distancing was detrimental to adolescent mental health; however, questions remain about whether these impacts were disproportionate in adolescents compared to other age groups, attributable specifically to social isolation rather than other pandemic-related stressors and persistent long-term. Longitudinal effects will likely become more apparent as researchers continue to track mental health over time.

1.3.4 Investigating Sensitive Periods

Given the precise definition of a sensitive period, the current literature faces challenges in definitively establishing adolescent sensitive periods in humans – particularly for the complex, multifaceted functions. Researchers have studied sensitive periods primarily using deprivation paradigms which came about from highly controlled, experimental animal research into early developing sensory functions. For example, the Hubel and Wiesel (1965) study used experimental deprivation of visual input to assess when the experience of visual input was required for normal vision to develop. Analogous "natural experiments" in humans have provided initial insights, including visual deprivation in infants with cataracts, caregiving deprivation in internationally adopted children and, a less controlled but nonetheless informative example, social distancing experienced by adolescents during the COVID-19 pandemic. However, studying potential sensitive periods in these later developmental periods presents particular challenges. Disentangling the specific effects of *adolescent* experiences becomes increasingly difficult when accounting for earlier developmental influences, normative developmental trajectories and genetic predispositions, particularly when attempting to track these effects longitudinally (Cheng et al., 2024).

Contemporary perspectives advocate for employing alternative approaches (Gabard-Durnam and McLaughlin, 2020). For example, in substitution paradigms researchers can explore the impact of impoverished versus enriched environments, as well as individual differences in stress exposure, on the timing and characteristics of sensitive periods. Computational modelling can simulate developmental trajectories and test theoretical frameworks (Frankenhuis and Walasek, 2020). The application of statistical methods, such as structured life course modelling, to large-scale longitudinal datasets offers another means aimed at disentangling sensitive period effects from other developmental influences such as recency or accumulation of experiences (Cheng et al., 2024). Another approach is to examine the efficiency of information acquisition at different ages – that is, learning (Knoll et al., 2016; provided that this increased efficiency of learning is specific, discrete and long-lasting as per the criteria for being defined as a sensitive period). Beyond basic scientific understanding, investigating adolescent sensitive periods has significant practical application in promoting healthy development and addressing adolescent

mental health challenges. Identifying sensitive periods enables the optimisation of timing and design for educational, psychological and therapeutic interventions to increase their impact. Furthermore, recognising the unique and lasting effects of adolescent experiences might guide policies towards creating supportive environments and reducing adolescent-specific risk factors.

1.3.5 Adolescence as a Window of Opportunity

Regardless of whether adolescence can be formally classified as a sensitive period, adolescence is recognised as a time of significant flux in physical, cognitive, neural and socioemotional domains. Across science and society, there is widespread consensus that adolescence is an important developmental window that confers both opportunity for the effects of positive experiences to promote wellbeing (such as getting an education, engaging in healthy relationships, etc.) *and* vulnerability for the effects of negative experiences (such as trauma, social exclusion, etc.) to reduce wellbeing (Sisk and Gee, 2022; Figure 1.1). Importantly, this perspective is bolstered by evidence that the human brain continues to change and develop into the third decade of life.

Figure 1.1 Adolescence as a Sensitive Window



Note. Adolescents are simultaneously sensitive to negative experiences (like natural disasters or trauma - left) and to positive experiences (such as learning opportunities - right). Therefore, adolescence is a developmental period characterised by both vulnerability and opportunity.

1.4 The Adolescent Brain

The human brain undergoes remarkable changes throughout adolescence. Contrary to earlier beliefs that brain development was largely complete by late childhood, leaving adolescence as

a neurobiologically static period (Blakemore, 2012), we now know this is not the case. While the brain reaches its approximate adult size around age nine, significant maturation and internal reorganisation continues up to approximately age 25. Seminal longitudinal studies beginning in the late 1990s provided compelling evidence of substantial changes in brain composition and connectivity throughout adolescence and into adulthood (Casey et al., 2008b; Giedd et al., 1999; Park et al., 2022; Sowell et al., 1999; Spear, 2000). These initial findings challenged previously accepted views and led to a surge of research over the past three decades focused on understanding the specific nature and implications of adolescent brain development.

1.4.1 Biological Bases of Brain Development

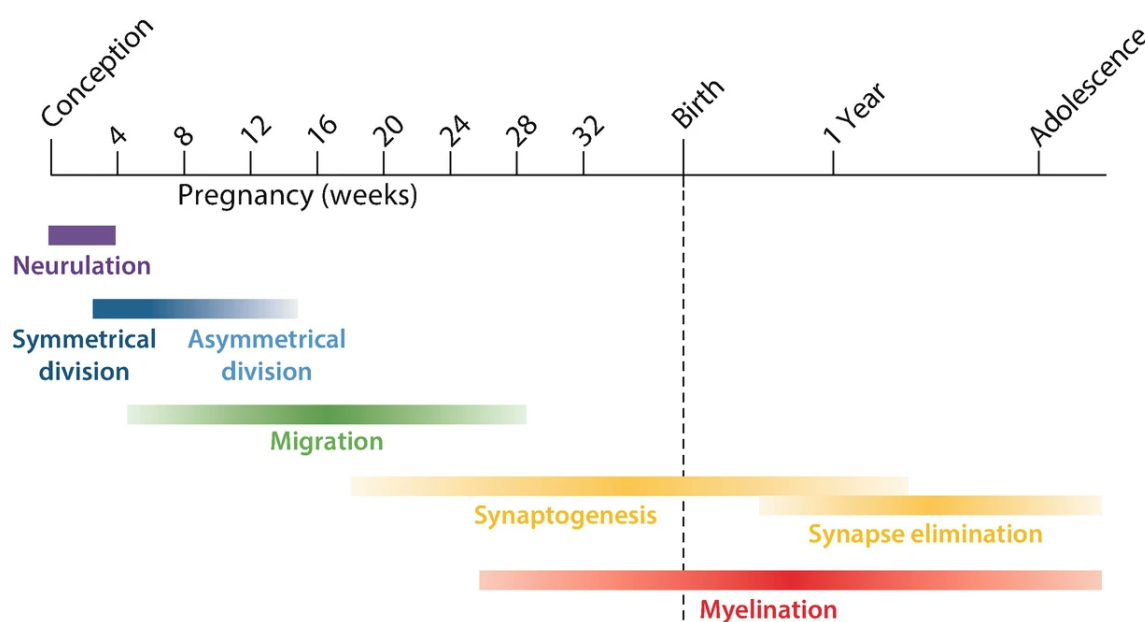
The development of the human brain begins around the third week of pregnancy and continues at least through late adolescence and, arguably, throughout life (Stiles and Jernigan, 2010). Brain development can be broken down into several fundamental stages at the cellular level (Figure 1.2) including: 1) Neurogenesis: the process by which new neurons are formed and multiply; 2) Neural Differentiation and Migration: the transformation of undifferentiated brain cells into specific cell types and their movement into distinct regions; 3) Synaptogenesis: the creation of connections between neurons both within and across regions; 4) Synaptic Refinement: the selective elimination and remodelling of neural connections; and 5) Myelination³: the process of insulating axons with a lipid-rich membrane to increase the efficiency of action potential transmission.

By the time a child is born, stages 1 – 2 are largely complete (Tau and Peterson, 2010). During infancy, continued synaptogenesis means that connections between neurons proliferate and reach levels that far exceed that of adult brains (Innocenti and Price, 2005). In childhood, a major period of synaptic pruning begins. During this process, the most useful neurons, synapses and dendrites are preserved and others are eliminated (Seeman, 1999). This process of elimination and refinement continues into the teen years. One of the most protracted cellular processes is myelination, which increases the speed, efficiency and stability of a neural circuit. Myelination begins in utero and continues through adolescence and adulthood (Hill et al., 2018).

It is important to note that these stages are comprised of a complex, dynamic, sequential and yet temporally overlapping series of cellular events that are both genetically determined and environmentally influenced (Tau and Peterson, 2010). Importantly, the timing of these cellular processes is not uniform across regions of the brain. Brain development follows a caudal-to-rostral progression, adhering to a fundamental principle of central nervous system

³It is important to acknowledge that other neurodevelopmental processes also exist, such as changes to axonal diameter (Genc et al., 2023).

Figure 1.2 Cellular Stages of Brain Development



Note. Overview of the approximate time course of essential cellular processes of brain development.

Source: Reproduced from Strüber and Roth (2023) with permission from Springer Nature.

maturation (Strüber and Roth, 2023): caudal regions, such as those in the spinal cord governing basic reflexes, develop earlier, whilst rostral structures associated with more complex functions mature later. For example, cortical regions of the frontal lobe are the final areas to reach full maturation. During adolescence, cellular processes at work primarily involve synaptic refinement and myelination across various slowly maturing brain regions. Synaptic refinement that reorganises and fine-tunes neural circuits as a result of *experience* is known as neuroplasticity.

1.4.1.1 Neuroplasticity During Adolescence

Neuroplasticity is the brain's ability to adapt and change its structure, function and connectivity in response to experiences, learning and environmental influences (Puderbaugh and Emmady, 2025). Compared to precocial species (e.g., ducks, giraffes) that function independently at birth with innate, hard-wired neural circuits, humans are altricial, born in a relatively underdeveloped state requiring prolonged postnatal development. Human brain development is characterised by extensive synaptogenesis during prenatal and early postnatal periods, creating an initially overconnected neuronal network. This overconnection enables a complex and extended period of refinement, or synaptic plasticity, during which neural pathways are directly shaped by environmental inputs. Synaptic plasticity refers to a set of mechanisms that mediate

the activity-dependent strengthening or weakening of neuronal connections at the level of the synapse (Citri and Malenka, 2008; Tau and Peterson, 2010). In other words, synaptic connections that are active are strengthened and those that are unused are eliminated (Changeux and Danchin, 1976). The resulting protracted neurodevelopmental trajectory affords humans exceptional behavioural flexibility and adaptive capacity, allowing individuals to acquire specialised knowledge unique to their particular cultural, linguistic and social environments.

The human brain retains a level of plasticity throughout the lifespan, enabling the learning of new information. However, heightened plasticity is observed during specific developmental periods (sensitive periods). Evidence suggests that the onset, maintenance and closure of sensitive periods of brain development are biologically orchestrated (Gabard-Durnam and McLaughlin, 2020; Paus et al., 2008; Petanjek et al., 2011) and appear largely conserved across species (Reh et al., 2020; Sydnor and Satterthwaite, 2023). Molecular pacers and triggers initiate sensitive period plasticity, including the development of a subset of inhibitory GABAergic interneurons, known as parvalbumin-positive interneurons (Hensch, 2018). Heightened plasticity is observed only after these interneurons have reached a certain level of maturity, a process partly driven by experience. Therefore, the timing of sensitive periods are thought to be flexible rather than fixed, influenced by both experiential and biological factors (Fuhrmann et al., 2015; Sydnor and Satterthwaite, 2023). For example, animal research has shown that this timing depended on whether animals were raised in a stimulating or deprived environment (for review see Werker and Hensch, 2015). Animals raised in standard laboratory cages had a shorter sensitive period for binocular vision that ended at a young age. However, animals raised in enriched environments with social interaction and physical/cognitive stimulation maintained a highly receptive visual cortex into adulthood.

The adolescent brain is characterised by a high degree of neuroplasticity, second only to infancy in humans in its capacity for change (Jernigan et al., 2011; Vijayakumar et al., 2016). With the onset of puberty, adrenal and gonadal hormones appear to have activating and organising effects on the brain (Goddings et al., 2019; Laube et al., 2020; Piekarski et al., 2017b; Sisk, 2017). Recent research provided the first evidence that ovarian hormones organise the neocortex during puberty in an animal model (Piekarski et al., 2017a). The study examined inhibitory and excitatory post-synaptic signals in the anterior cingulate cortex of female mice, and revealed that inhibitory neural activity increased at the onset of puberty. This shift correlated with differences in performance on a reversal learning task. Follow up experiments revealed that removing the ovaries before puberty prevented the normal increase in inhibitory signalling, but hormone replacement restored it. Further, administering estradiol and progesterone to prepubertal mice accelerated the maturation of inhibitory circuits by increasing GABA release. Importantly, mice given early hormone treatment also showed adult-like performance in reversal

learning tasks and the neural effects were region specific. Though these findings were only in female mice, they suggest that pubertal hormones trigger the onset of a sensitive period of neuroplasticity. Relatedly, a study using pharmacological fMRI identified age-related increases in inhibitory relative to excitatory balance in specific cortical regions during adolescence, which is consistent with the idea of adolescent sensitive period emergence (Takesian and Hensch, 2013).

At the conclusion of a sensitive period, neural circuits in the brain stabilise, thereby increasing processing efficiency whilst restricting further change. This stabilisation serves an adaptive function. The consolidation that occurs at the end of a sensitive period both protects neural circuitry from potentially disruptive environmental influences and facilitates the consolidation of learned skills. Similarly to the onset of sensitive period plasticity, its offset is thought to be controlled by molecular "brakes", which limit adult plasticity (Takesian and Hensch, 2013). Perineuronal nets (PNNs) are specialised extracellular matrix structures responsible for synaptic stabilisation in the adult brain (Fawcett et al., 2019). In animal models, research has shown that closure of sensitive periods in sensory cortices coincides with perineuronal net (PNN) expression (Drzewiecki et al., 2020). PNN density was found to increase across adolescence in the male rat medial prefrontal cortex (mPFC) and both male and female rats showed an increase in the total number of mPFC PNNs during adolescence. Another mechanism associated with the closure of sensitive period neuroplasticity is myelination (Boghdadi et al., 2018; Gerber et al., 2009; Paus et al., 2008; Petanjek et al., 2011). Myelin, the fatty insulating layer surrounding neuronal axons, facilitates efficient electrical signal transmission. Additionally, its protein composition hinders axon growth, restricting structural modifications after the sensitive period (Fletcher et al., 2021; Sydnor and Satterthwaite, 2023; Werker and Hensch, 2015). Consequently, myelination serves as a physical "brake" on neuroplasticity. Protracted myelination might suggest insight into the length and timing of sensitive windows of heightened neuroplasticity. In humans, myelination continues to increase throughout adolescence and beyond (Larsen et al., 2023; Paus et al., 2008; Simmonds et al., 2014), as shown by studies investigating brain structure using magnetic resonance imaging (MRI).

1.4.2 Structural Brain Development

Although many of the methods used to study cellular mechanisms of brain development in animals (microscopy, electrophysiology) cannot be applied to the living human brain, the adoption of MRI for neuroscience research in the 1990s enabled *in vivo* investigation of the developing brain, which was previously limited to post-mortem samples. Structural MRI enables the quantification of several neuroanatomical features which can be interpreted within the framework of known cellular developmental processes. Specifically, it allows for analysis

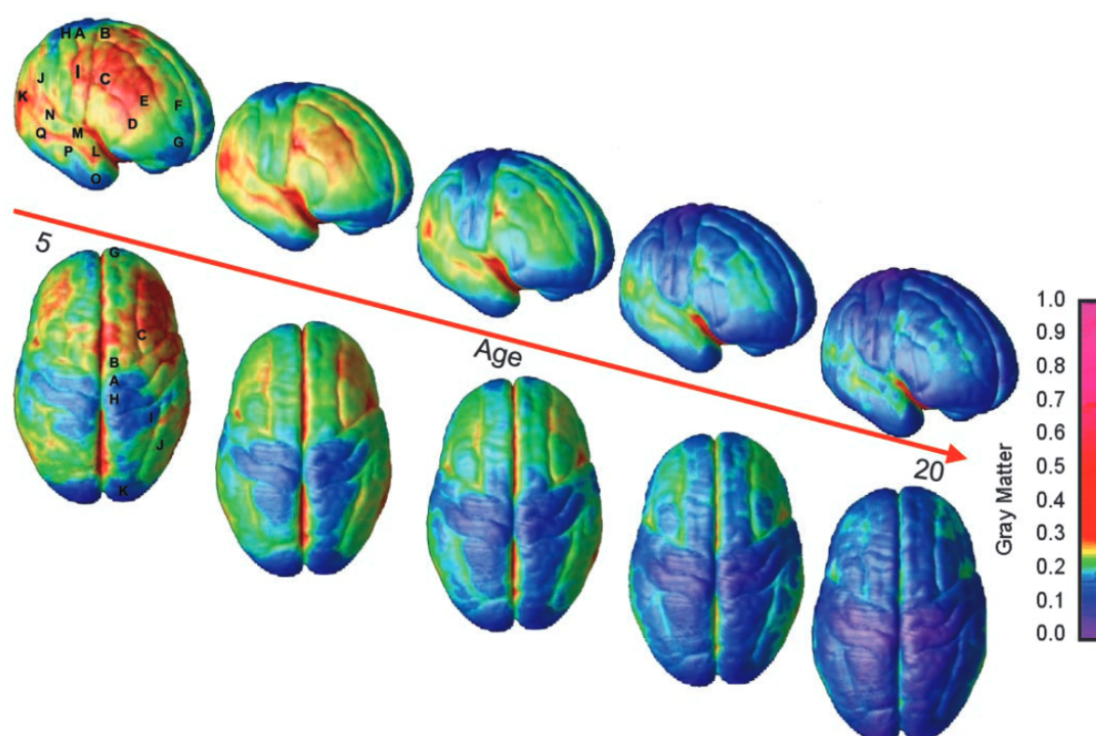
of the brain's grey and white matter structures. MRI signals differ between these tissue types due to the higher concentration of cell bodies in grey matter compared to white matter, which mainly consists of myelinated axons and supporting glial cells. Morphometric methods assess the volume of grey matter regions including subcortical structures, as well as the volume, thickness, and surface area of the cortex. These measures are collectively known as brain *macrostructure*.

Longitudinal studies with large, diverse samples investigating the cerebral cortex in adolescent humans have documented childhood increases in cortical grey matter volume and thickness, followed by progressive decreases throughout adolescence (Ducharme et al., 2015; Mills et al., 2014; Raznahan et al., 2011; Tamnes et al., 2013; Wierenga et al., 2014). Surface area follows a similar pattern, albeit less pronounced. The volume reduction observed between ages 7 and 29 is primarily attributed to cortical thinning. This developmental pattern was originally thought to reflect synaptic proliferation followed by synaptic pruning (Lago et al., 2017; Liu et al., 2022; Park et al., 2022; Richards et al., 2012; Steinberg, 2010). However, it is likely that declines in apparent cortical grey matter volume are more substantially influenced by concomitant increases in underlying white matter, as axons previously classified as "grey matter" become myelinated across development and therefore reclassified as "white matter" using structural MRI (Tamnes et al., 2017, 2013; Vijayakumar et al., 2016).

Patterns of change in brain morphometry are widespread, nonlinear and regionally variable – meaning that not every brain region matures at the same time (Frangou et al., 2022; Tamnes et al., 2017). An important study tracked the anatomical progression of human cortical grey matter development from ages 4 to 21 by obtaining structural MRI scans from 13 typically developing children every two years for 8 – 10 years (Gogtay et al., 2004; Figure 1.3). Results showed that higher-order association cortices mature after the development of lower-order somatosensory and visual cortices. The prefrontal cortex is among the latest brain regions to fully mature, exhibiting pronounced structural changes into the third decade of life (up until approximately age 25; Giedd et al., 1999; Kolk and Rakic, 2022; Manitt et al., 2013; Sowell et al., 1999; Spear, 2000). Subcortical structures also show evidence of development during adolescence. One study investigated developmental trajectories by analysing three independent longitudinal datasets of participants aged 8 – 22 years (Herting et al., 2018). The study identified generalisable, age-related patterns of change across adolescence in the amygdala, putamen and nucleus accumbens. Significant sex differences emerged, with males showing steeper increases in curvilinear amygdala growth compared to females. Additionally, females exhibited decreases in nucleus accumbens and putamen volume with age, whereas males demonstrated either no change (nucleus accumbens) or less pronounced decreases (putamen). Another study directly compared the developmental trajectories of subcortical regions and the prefrontal cortex at an

individual level in participants aged 7 – 30 years (Goddings et al., 2014). Results revealed that most individuals exhibited earlier structural maturation in the amygdala and/or nucleus accumbens relative to the prefrontal cortex. This developmental mismatch between subcortical and prefrontal regions (discussed further in Section 1.4.3) confirmed previous cross-sectional findings (for review see Somerville et al., 2010).

Figure 1.3 Structural Brain Maturation



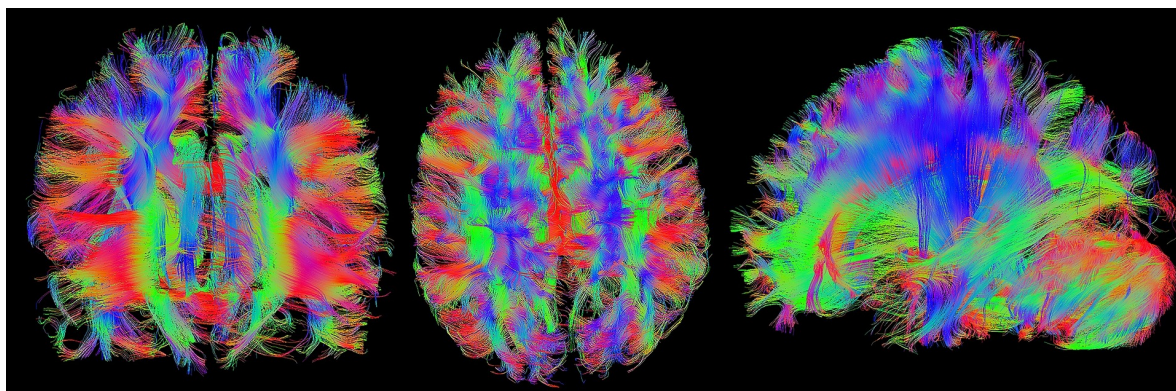
Note. Right lateral and superior views depicting the progression of grey matter maturation across the cerebral cortex from ages 5 to 20 years. The colour bar represents grey matter volume, with darker hues (blue/purple) indicating reduced grey matter volume or cortical thinning, which signifies brain maturation. *Source:* Reproduced from Gogtay, N., Giedd, J. N., Lusk, L., Hayashi, K. M., Greenstein, D., Vaituzis, A. C., Nugent, T. F., 3rd, Herman, D. H., Clasen, L. S., Toga, A. W., Rapoport, J. L., & Thompson, P. M. (2004). Dynamic mapping of human cortical development during childhood through early adulthood. *Proceedings of the National Academy of Sciences of the United States of America*, 101(21), 8174–8179. <https://doi.org/10.1073/pnas.0402680101>. Copyright (2004) National Academy of Sciences.

In contrast to brain macrostructure, which focusses on the large-scale structural organisation of brain anatomy, brain *microstructure* focuses on tissue properties like cell density, myelination and axonal organisation. Despite constituting 50% of brain tissue, research into

brain microstructure has historically received less attention. Given recent research implicating myelination as a potential marker for the offset of heightened developmental neuroplasticity, interest has increased in using neuroimaging methods to probe microstructural features in the living human brain. Cortical myelination can be indirectly quantified in humans with multiple MRI measures, for example, the water-macromolecule magnetisation transfer ratio, the T1- to T2-weighted ratio, and the T1-based grey matter-white matter contrast (GWC). These techniques have recently been used to demonstrate increases in myelin content in most brain regions during adolescence (Geeraert et al., 2019; Genc et al., 2023; Larsen et al., 2023; Paquola et al., 2019).

Diffusion tensor imaging (DTI) tractography has emerged as a separate MRI technique for mapping the architecture of white matter tracts in the living human brain. This approach depicts the movement of water molecules along major white matter pathways (Mirza-Davies and Harrison, 2019). In 1994, Bassler et al. showed that diffusion tensor imaging (DTI), using multiple diffusion gradients, could determine the main three-dimensional direction of white matter fibres within each MRI voxel, a concept known as the diffusion tensor. This tensor has enabled the visualisation of major white matter tracts in humans (various techniques have since been developed; Froeling et al., 2016; Jones and Leemans, 2011; O'Donnell and Westin, 2011; Ressel et al., 2018; Soares et al., 2013). To illustrate white matter tracts, colour coded two-dimensional images are constructed (See Figure 1.4).

Figure 1.4 Diffusion Tensor Imaging (DTI)



Note. Whole-brain diffusion tensor imaging (DTI) tractography visualisation showing white matter fibre pathways in the human brain. Colours represent different fibre orientations. *Source:* Needpix (CC0/Public Domain).

Diffusion tensor imaging (DTI) studies have revealed microstructural changes in multiple white matter fibre tracts during adolescence (Lebel and Deoni, 2018; Lebel et al., 2012; Simmonds et al., 2014) and white matter volume has been found to exhibit largely linear age-

related increases (Bero et al., 2023; Dumontheil, 2016; Larsen and Luna, 2018). Increased age-related structural connectivity of white matter tracts is particularly evident in pathways linking the prefrontal cortex to other cortical regions and subcortical structures across adolescence (Park et al., 2022; Schmithorst and Yuan, 2010; Supekar et al., 2010).

1.4.3 Brain Function in Adolescence

1.4.3.1 Socio-Affective System

The adolescent brain not only exhibits structural differences from the brains of children and adults, but also shows substantial functional differences during this developmental period – especially in regions involved in affective and social processing. Subcortical structures, including the striatum (a key component of the reward system) and the amygdala (a structure implicated in emotional processing), show evidence of heightened reactivity to rewards and threats, particularly when these occur in social contexts. Studies using functional MRI have shown that the ventral striatum shows heightened sensitivity to rewards during adolescence (Galvan, 2010; Galván, 2013; Telzer, 2016). Using monetary reward-based tasks, research has revealed exaggerated neural activation in the ventral striatum in adolescents compared to children and adults (Galván and McGlennen, 2013). In participants aged 13 – 22 years, reward-related responses in the nucleus accumbens to having one's own content "liked" on Instagram were highest at around age 16 – 17 years⁴ (Sherman et al., 2018). When viewing social-emotionally salient stimuli, such as photos of emotional faces, activity in the amygdala decreased from adolescence into emerging adulthood (between 10 and 24 years of age) for both positive and negative social cues (Vijayakumar et al., 2019; Vink et al., 2014), suggesting heightened neural sensitivity to social-emotional information during adolescence compared to adulthood. Further, compared to children (aged 10 – 12 years), adolescents (aged 14 – 17 years) showed greater neural activity (midfrontal theta power as measured by electroencephalography [EEG]) to both social exclusion and threats of exclusion (Tang et al., 2021). Being rejected based on one's online profile picture resulted in increased activity in the medial prefrontal cortex in children aged 7 – 10 years (Achterberg et al., 2017) and in late adolescents/emerging adults aged 18 – 27 years⁵ (Achterberg et al., 2016).

⁴Some studies have also reported diminished activation in reward regions in adolescents (Bjork et al., 2010) or differential responses during various stages of reward processing, such as anticipation versus receipt (Geier and Luna, 2009).

⁵It should be noted there were no comparison age groups in these studies.

1.4.3.2 The Social Brain

Social-cognitive abilities which rely on social brain regions—including perspective-taking, emotional understanding, navigation of complex social interactions and relationship formation—continue to develop throughout adolescence. The social brain includes a core set of regions that studies have consistently identified as being involved in tasks of social cognition, including the posterior superior temporal sulcus (pSTS), the temporo-parietal junction (TPJ) and the dorsal medial prefrontal cortex (dmPFC; Blakemore, 2012). Research has identified adolescence as a period of significant functional maturation in the social brain (for review see Andrews et al., 2021). For example, studies have shown age-related differences in the activation of social brain regions during mentalising tasks (Gweon et al., 2012; Mukerji et al., 2019; Saxe et al., 2009), social brain regions increasingly participate in processing social emotions throughout adolescent development (Blakemore and Mills, 2014) and age-related improvements in emotion regulation have been associated with reduced amygdala activation (Silvers et al., 2017; Stephanou et al., 2016) and inverse coupling (i.e., negative functional connectivity) between the ventromedial PFC and the amygdala (Gee et al., 2013). Further, a recent longitudinal study showed that neural responses in the social brain increased linearly during early to mid-adolescence during both self and other evaluations (Cosme et al., 2022). Self-evaluation of social information, particularly related to social status, was associated with greater activity in social brain regions during the transition from early to mid-adolescence (Cosme et al., 2022).

1.4.3.3 Cognitive Control System

The literature suggests that the prefrontal cortex plays a key role in cognitive control (Larsen and Luna, 2018; Luna et al., 2010; Steinberg, 2010). Cognitive control exhibits a remarkably consistent developmental trajectory characterised by rapid advancement from late childhood to mid-adolescence (ages 10~15) before stabilising to adult levels in late adolescence (ages 18~20; Tervo-Clemmens et al., 2023). Studies investigating prefrontal cortical activity with regard to cognitive control in adolescents have yielded seemingly contradictory findings of both age-related increases (Bunge et al., 2002; Rubia et al., 2000; Tamm et al., 2002) and decreases (Rubia et al., 2007) in its involvement. When performance levels are matched, dorsolateral prefrontal cortex (DLPFC) activation most consistently decreases with age (Tamm et al., 2002). This greater activation in younger adolescents might indicate that achieving adult-level performance requires increased effort, and subsequently more reliance on the DLPFC. Alternatively, increased activity in the prefrontal cortex might reflect immaturity of the prefrontal cortex in younger adolescents, leading to more extended processing and

consequently higher activity compared to adults. Further, some research indicates an inverted U-shaped pattern of activation, where adolescents exhibit heightened activity in the prefrontal cortex compared to both children and adults when completing tasks requiring cognitive control (Ciesielski et al., 2006; Luna and Sweeney, 2001) suggesting adolescence as a distinct phase of performance increases paralleled by adolescent-specific differences in prefrontal cortical activation.

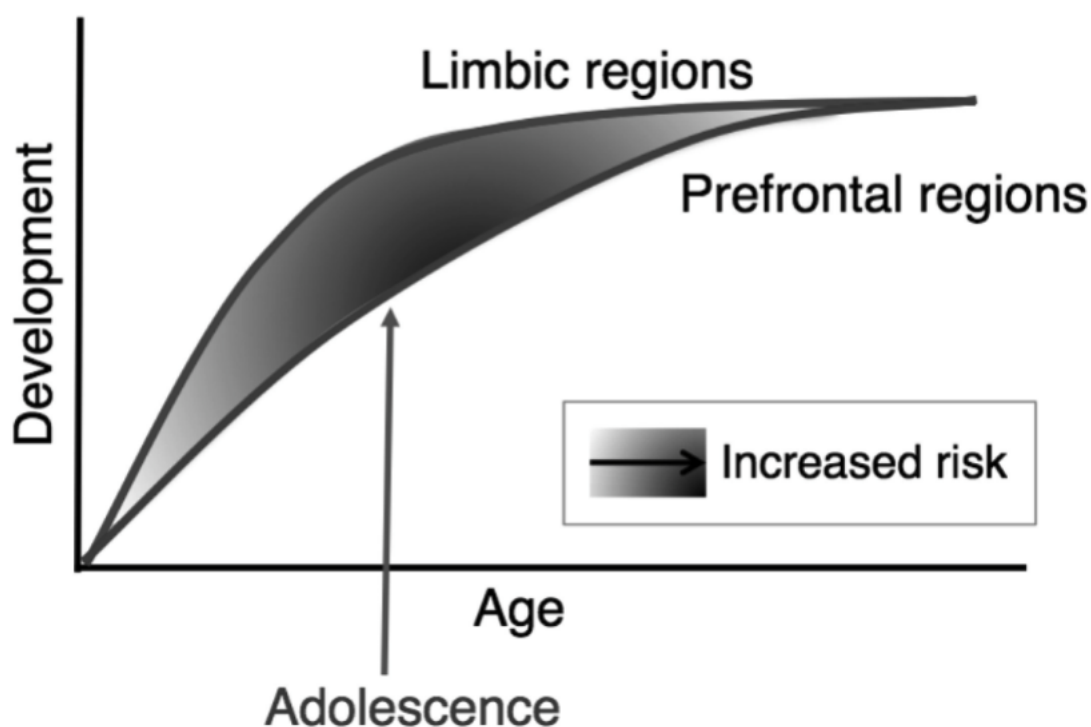
1.4.3.4 Theories of Adolescent Neurodevelopment

The function of the prefrontal cortex is closely intertwined with the socio-affective circuitry (Casey et al., 2025, 2008b; Goddings et al., 2019; Larsen et al., 2020). As described in Section 1.4.2, the prefrontal cortex is one of the last brain regions to reach structural maturity (Tamnes et al., 2017). Cortical grey matter development follows a regional progression, where areas responsible for primary functions mature earlier than those dedicated to complex and integrative tasks. Researchers have proposed that different regional rates of brain maturation create a *maturational imbalance*⁶ (Casey et al., 2008a; Ernst et al., 2006; Somerville et al., 2010; Steinberg, 2008); Figure 1.5). Theories of maturational imbalance propose that the early development of subcortical structures (part of the socio-affective system), coupled with the protracted development of the prefrontal cortex (part of the cognitive control system), contribute to adolescent behaviours characteristic of social and affective sensitivity such as heightened risk taking (Chein et al., 2011), impulsivity, sensation seeking and emotionality.

In recent years, researchers have shifted towards more circuit-based accounts of functional brain development (Casey, 2015). Rather than focusing on brain regions as discrete functional systems, these approaches emphasise evolving connectivity patterns. Functional connectivity is assessed by measuring the temporal correlation between the activity of spatially distinct brain regions (Goddings et al., 2019; Vértes and Bullmore, 2015). Numerous resting state fMRI studies have demonstrated age-related changes in functional connectivity that reflect a transition from more localised and less differentiated functional architecture in childhood towards a more distributed and integrated network organisation in adolescence and adulthood (Bero et al., 2023; Galván, 2021; Park et al., 2022). This functional segregation is thought to allow for greater specialisation of brain regions, supporting the coordination of diverse cognitive processes necessary for complex behaviours (Cole et al., 2014; Galván, 2021; Marek et al., 2015). One review (Casey et al., 2019) proposes that circuit-based studies suggest that the development of the emotional brain during adolescence involves a transition from

⁶The maturational imbalance theory (Casey et al., 2008a) includes several variations, such as the dual-systems model (Steinberg, 2008), the developmental mismatch theory (Somerville et al., 2010) and the triadic model (Ernst et al., 2006).

Figure 1.5 Maturation Imbalance Theory



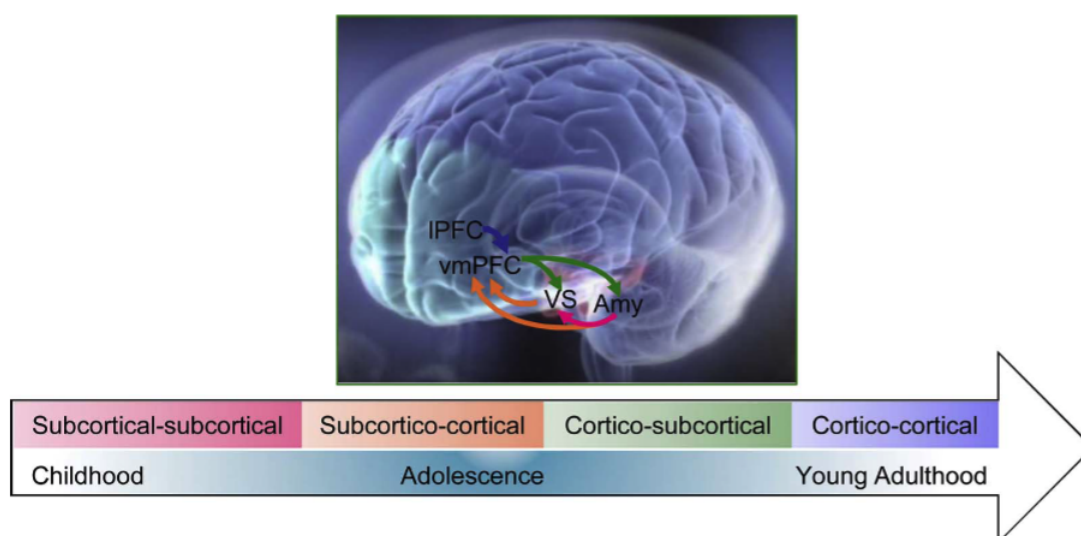
Note. Model of heightened affective and incentive-based behaviour in adolescence. The early maturation of subcortical regions (including the amygdala and striatum) combined with the late maturation of the prefrontal cortex predicts a period of maturational imbalance during adolescence.

Source: Reproduced from *Brain and Cognition*, Volume 72, Somerville, L. H., Jones, R. M., & Casey, B. J. (2010) *A time of change: behavioral and neural correlates of adolescent sensitivity to appetitive and aversive environmental cues*. Copyright (2010) Elsevier.

primarily subcortical emotional reactivity towards increasing cortical regulation, driven by specific, sequential changes in functional connectivity between brain regions – developing from primarily subcortico-subcortical to subcortico-cortical to cortico-subcortical and finally to cortico-cortical connectivity across childhood to adulthood (Figure 1.6). Other researchers have moved away from imbalance/immaturity models altogether (UCLA Center for the Developing Adolescent 2022), emphasising instead the unique adaptability of the adolescent brain and its emerging cognitive capabilities. This perspective frames adolescence as a unique period, while acknowledging that brain development should not be characterised as simply "incomplete" before age 25⁷.

⁷Brain maturation continues throughout adulthood without a definitive "completion" point.

Figure 1.6 Emotion Circuitry Reorganisation



Note. Changes in functional brain circuitry across the lifespan, showing a developmental trajectory from subcortical to cortical regions. The colours indicate regional connectivity shifts from childhood through adolescence to adulthood: pink (subcortico-subcortical), orange (subcortico-cortical), green (cortico-subcortical) and blue (cortico-cortical). Brain regions include the ventromedial prefrontal cortex (vmPFC), lateral prefrontal cortex (IPFC), ventral striatum (VS) and amygdala (Amy). *Source:* Reproduced from *Neuroscience Letters*, Volume 693, Casey, B. J., Heller, A. S., Gee, D. G., & Cohen, A. O. (2019) *Development of the emotional brain*. Copyright (2019) Elsevier.

1.5 Learning During Adolescence

Given the heightened affective and social sensitivity displayed by adolescents both behaviourally and neurally and the close connection between learning and neuroplasticity⁸, it is important to understand how affective and social *learning* are different during adolescence. This section focuses on associative learning due to its experimental and computational tractability, revealing an intricate and complex picture.

1.5.1 Classical Conditioning – Pavlovian Learning

During Pavlovian learning (also called classical conditioning), organisms learn that previously neutral stimuli (e.g., a bell sound, a light, a location) are predictive of a reward or threat (Pavlov, 1927; Rescorla and Wagner, 1972). This form of learning is relatively basic because

⁸Many neurobiologists believe that synaptic plasticity is the basis of learning (Goda and Stevens, 1996; Morris, 1990)

the associations are learned by simple exposure to repeated pairings between neutral stimuli and rewards or threats; that is, the organism does not need to engage in any overt choice. Humans, as well as animals, single-celled organisms (Gelber, 1952), and even plants (Gagliano et al., 2016) have demonstrated the ability to establish Pavlovian associations. Pavlovian learning changes across adolescent development in several ways.

1.5.1.1 Reward Learning

Rodent studies show heightened Pavlovian learning of food and drug rewards in adolescent compared to adult rats (Brenhouse and Andersen, 2008; Zakharova et al., 2009). Adolescent rats also show increased activity in dopamine neurons in the substantia nigra – a component of the striatal reward pathway – compared to adult rats during Pavlovian reward learning (McCane et al., 2021; Sturman and Moghaddam, 2012). In human adolescents, Pavlovian reward learning has been studied using monetary rewards or positive written, verbal, or visual feedback. Older adolescents showed faster response times when learning to respond to stimuli that predicted rewards, compared to children and adults (Davidow et al., 2019). In a separate study, items paired with rewarding feedback were better recalled by adolescents on a later memory test, compared to adults (Davidow et al., 2016), and this difference was associated with stronger functional connectivity between the hippocampus and the striatum during reward receipt. Elements of "unlearning", called extinction, have also been found to differ between adults and adolescents. For example, one study showed that, once adolescent rats learned to associate a cue with a reward, it was more difficult for them than for adults to suppress their learned reward response, even if the cue was no longer predictive of a reward (Meyer and Bucci, 2016). Social rewards can powerfully guide Pavlovian learning, and this type of social reward learning also seems to vary with age. For example, rodents learn to prefer locations that had previously been paired with a conspecific, and this socially conditioned place preference peaks in mice in mid-adolescence (Cann et al., 2020), before declining into adulthood (Nardou et al., 2019).

Evidence suggests that, although Pavlovian responding by adolescents might be more sensitive than that of adults, it might not be as specific; that is, it might discriminate less well between different reward probabilities or magnitudes. In one study, adolescent rats displayed a Pavlovian reward learning advantage relative to adult rats when cues were reinforced probabilistically (i.e., intermittently with some probability) but not deterministically (continuously) (Meyer and Bucci, 2016). In addition, whereas adult rats learned proportionally about the probability of reward, adolescent rats did not display this fine-tuning (Meyer and Bucci, 2016). In line with this, another study found that adolescent rats responded equally to both weakly and strongly predictive reward cues, whereas adult rats flexibly adjusted their pattern of responding based on

the expected likelihood of reward (Marshall et al., 2020). Reduced specificity in social reward learning has also been found in human adolescents, who discriminated less between different amounts of positive social feedback than children and adults (Jones et al., 2014). In the same study, adolescents showed greater neural activity than children or adults during social rewards in regions associated with motivation and action (putamen, insula, and supplementary motor cortex).

1.5.1.2 Threat Learning

Several studies have shown comparable learning of Pavlovian threat responses (also called "fear learning") in children, adolescents, and adults (in both humans and animals) (Den et al., 2015; Ganella et al., 2017; Waters et al., 2017; Zbukvic et al., 2017). In line with Pavlovian reward learning, however, some studies have shown that adolescents display diminished extinction of learned threat responses, compared to both adults and pre-adolescents, in human and rodent models (Den et al., 2015; Johnson and Casey, 2015; Morriss et al., 2019; Pattwell et al., 2012). Although there has been contradictory evidence regarding this finding (Chocyk et al., 2014; Ganella et al., 2017; Perry et al., 2020; Waters et al., 2017), it has been proposed that it is not the ability to extinguish threat responding per se, but rather the ability to retain threat response extinction, or extinction retention, that is attenuated in adolescence (Gerhard and Meyer, 2021). For example, in humans and rodents, adolescents have shown a heightened relapse of threat responding (less threat extinction retention) relative to both juveniles and adults (Baker et al., 2016; Johnson and Casey, 2015; Kim et al., 2011), and reductions of extinction retention have been associated with age-related changes in fronto-amygdala circuitry in adolescence (Odrizola and Gee, 2021).

Research on human adolescent threat learning often employs social stimuli such as a face combined with an aversive scream (Den et al., 2015; Ganella et al., 2017; Haddad et al., 2011; Morriss et al., 2019; Roesmann et al., 2022a). Studies using social stimuli have frequently reported similar age-related reductions in extinction and/or extinction retention (in adolescents) as those using non-social stimuli (Johnson and Casey, 2015; Pattwell et al., 2012; Waters et al., 2017). However, there has so far been no systematic comparison of the effects of different stimulus types (social versus non-social) on adolescent threat learning to determine whether social threats (like social rewards) hold particular significance for adolescents. In the absence of direct threat experiences, threat associations can also be acquired by observing a learned threat response in another individual (observational learning). This type of social learning is known as vicarious threat learning (sometimes called "vicarious fear learning"). In rodent models, male adolescent mice show higher vicarious threat learning than male adult mice, although

this age effect might not be uniquely social because direct threat learning was also higher in adolescent mice (Keum et al., 2016).

Evidence from Pavlovian threat learning further supports the proposal that this period is associated with increased sensitivity and decreased specificity. Adolescent mice overgeneralise learned threat associations compared to adult mice (Ito et al., 2009), with lasting consequences. In one study, threat associations learned in adolescence delayed the normative development of adult threat discrimination (Müller et al., 2018). Human adolescents show reduced discrimination between learned threat and safety cues, and tend to overgeneralise their threat response and respond to all cues (even neutral cues) as if they are more threatening (Klein et al., 2021; Roesmann et al., 2022b). Threat generalisation in humans has been shown to decrease linearly between 8 and 17 years of age (Reinhard et al., 2021), suggesting changes in discriminative threat learning processes in adolescence. Relatedly, adolescent humans overgeneralised their threat response compared to adults during vicarious threat learning, and rated a threat cue as significantly more aversive even before faux electrodes were attached (Skversky-Blocq et al., 2021a,b). Another study found that participants aged 6 – 17 years vicariously learned from threats experienced by a parent over threats experienced by an unfamiliar adult (Silvers et al., 2021).

1.5.2 Operant Conditioning – Instrumental Learning

The evidence reviewed above suggests that, in Pavlovian learning, adolescents frequently show heightened learning relative to adults, possibly owing to heightened affective and social sensitivity. The evidence suggests that the same might not be true for instrumental learning (also called operant conditioning). Like Pavlovian learning, instrumental learning requires participants to learn the association between a novel cue and a valenced outcome such as a reward or a punishment. However, instrumental learning additionally involves decision-making because different choices are linked to different outcomes. For example, in a simple instrumental learning task, people might need to choose between two novel symbols, each leading to monetary gains or losses with a given probability. By repeatedly sampling the outcomes associated with each option, participants learn which option tends to be best. Although these learning environments might not be highly ecological, they allow researchers to computationally characterise learning and thus to investigate more precisely how the parameters that define learning change with age (Bolenz et al., 2019; Eckstein et al., 2021; Nussenbaum and Hartley, 2019). As articulated below, these studies suggest that lower specificity might lead adolescents to frequently (but not always) learn less efficiently than adults during instrumental learning.

Over the past decade, an increasing number of studies have addressed how instrumental learning changes with age. Many of these studies have found that adults typically outperform

adolescents in instrumental learning (Chierchia et al., 2022; Giron et al., 2022; Nussenbaum and Hartley, 2019; Xia et al., 2021). For example, adults tend to require fewer trials than adolescents to learn which options are best, make fewer errors, and thus learn more efficiently. Using social stimuli does not substantially offset this adult advantage. For example, learning from positive social feedback (Jones et al., 2014) or by observing others (Jepma et al., 2021; Rodriguez Buritica et al., 2019), as well as learning from others (Westhoff et al., 2021), about their cooperative behaviour (Westhoff et al., 2020) or preferences (Rosenblau et al., 2018), are all learning abilities that improve between adolescence and adulthood. One possible exception to this developmental trend is social influence or social contagion, which has typically been found to be heightened in adolescence relative to adulthood (Reiter et al., 2021).

A metaphor to describe age-related improvements in instrumental learning has been borrowed from a stochastic optimisation algorithm, called simulated annealing (Gopnik, 2020). When learning about reward contingencies in novel environments, this algorithm initially tests random guesses and makes large adjustments based on feedback. Like metals, which are more difficult to shape as they cool down, these adjustments become smaller and less likely to occur as the "guesses" of the algorithm become more accurate. In a computational comparison of human learning with this form of artificial learning, one study showed striking similarities in the way learning improves across human development and across different stages of simulated annealing (Giron et al., 2022). At the computational level, cooling down can be captured by a temperature parameter. Temperature specifies how precisely one's choices discriminate between positive and negative values and their magnitudes or probabilities. In other words, temperature regulates the extent to which option values direct choices. For low-temperature learning, a small difference in the outcomes associated with each option will direct choices towards the better option, while a larger difference might be necessary for higher temperature learning. Temperature can thus be interpreted as a measure of specificity in that it regulates how closely choices track reward and punishment contingencies. For example, learning with high temperature leads to more frequent deviations from an optimal choice, such as a known and liked restaurant or who to sit next to in a school cafeteria. This could occur because the learner does not fully know what they like and dislike, or it could more purposefully aim to explore novel alternatives. Conversely, learning with low temperature could lead to a more exploitative learning style, characterised by repeatedly choosing options that proved optimal in the past. Notably, across different experimental paradigms and different modelling approaches, many studies have shown that temperature decreases with age in adolescence (Chierchia et al., 2022; Eckstein et al., 2022a; Nussenbaum and Hartley, 2019).

Several non-mutually exclusive proposals have been developed to account for age-related improvements in instrumental learning and changes in specificity. One broad approach has

focused on facets of cognitive control that also improve in adolescence, such as working memory and non-verbal reasoning abilities. Abilities such as these facilitate instrumental learning by favouring the sustained attention necessary to monitor reward-related contingencies in stochastic environments (Niv et al., 2015), or by favouring the use of computationally more sophisticated forms of learning (Decker et al., 2015; Palminteri et al., 2016). For example, one study found that, between adolescence and early adulthood, age correlated both with non-verbal reasoning and inverse temperature in a reinforcement learning paradigm (Chierchia et al., 2022). However, this study, as well as others (Master et al., 2020; Nussenbaum et al., 2020), suggest that, although facets of cognitive control might explain part of the age differences in instrumental learning, they are unlikely to explain them entirely.

In addition to facets of cognitive control, many of which tend to develop steadily in adolescence before reaching an asymptote in early adulthood (Chierchia et al., 2019), other processes related to reward sensitivity develop non-linearly in adolescence. For instance, across cultures, sensation-seeking behaviours increase during the teenage years, are at their highest in the late teens, and then decrease throughout the twenties (Steinberg et al., 2018). Similarly, behavioural economics studies have found that adolescents display a uniquely high tolerance to ambiguity and uncertainty in risky decision-making (van den Bos and Hertwig, 2017), and, especially in situations involving peers, adolescents tend to accept riskier gambles than adults (Reiter et al., 2019). These considerations are consistent with the hypothesis that adolescents might learn more from positive than negative outcomes in instrumental learning, potentially leading to a behavioural form of optimism bias or a riskier learning style (Rosenbaum et al., 2022). However, over the past decade several studies have addressed this hypothesis and a consistent picture remains elusive (Eckstein et al., 2022b; Nussenbaum et al., 2022; Rosenbaum et al., 2022; van den Bos et al., 2012). For example, some studies have found that adults (as opposed to adolescents) tend to learn more from positive than negative feedback (van den Bos et al., 2012).

Indeed, a growing body of research suggests that people of all ages (as well as non-human primates and rodents) tend to learn more from positive than negative outcomes, and thus display a confirmatory learning style (Palminteri and Lebreton, 2022). Notably, simulations and experiments have shown that this asymmetry in learning frequently improves performance in instrumental learning, possibly because it buffers the impact of environmental noise, thus protecting people from excessive doubt when optimal options occasionally deliver suboptimal outcomes (Lefebvre et al., 2022). One study suggested that, although the magnitude of the positive versus negative learning discrepancy does not systematically vary with age, confirmatory learning increases with age between adolescence and early adulthood, while specificity increases (i.e., temperature decreases; Chierchia et al., 2022).

Moreover, although several of the studies described above suggest that performance in instrumental learning improves with age in adolescence, this might not always be the case. More specifically, both increasing specificity and confirmatory learning (as seen across adolescence) can optimise learning when evidence history is not misleading, but the same features can be problematic when it is. This can occur in at least two situations. First, even if one option has proved optimal in the past, this could change. In this case, continuing to exploit outdated evidence can be detrimental. This raises the hypothesis that adult advantages in instrumental learning might be reduced in more volatile environments. In line with this, several studies have shown that, especially in more volatile environments in which reward/punishment contingencies gradually or suddenly change (e.g., a previously optimal option becomes suboptimal), the adult advantage in instrumental learning is no longer observed (Chierchia et al., 2022) or can even reverse, thus favouring adolescents (Eckstein et al., 2022a; Lloyd et al., 2021). Second, in many cases the available evidence might not objectively favour any option. In such cases there is no way to improve performance, but continued attempts to interpret outcomes as evidence can consume cognitive resources. In line with this, one study showed that when reward and punishment history did not favour one option over the other (when participants were asked to repeatedly choose between two novel symbols that had the same chance of being rewarded/punished), adults took longer than adolescents to reach decisions, thus incurring greater cognitive costs in terms of time spent to reach the decision (Chierchia et al., 2022).

These findings are consistent with the notion that adult learning might be generally optimised for narrower tasks such as instrumental learning in stable environments, but that adolescent learning styles might be adapted for detecting novel solutions in more volatile environments for the purpose of exploration and innovation (Gopnik, 2020). Adolescents might have some learning advantages over adults in novel environments because they encounter such environments more frequently. Indeed, adolescence can be considered to be a stage of environmental volatility because of the gradual detachment from one's caregivers and exploration of new activities and new social and romantic relationships (Nelson et al., 2016). Under this lens, lower specificity in learning (or higher temperature) in adolescence could also be due to adolescents having less knowledge about themselves and the world than adults (in Bayesian terms, they have broader priors). In other words, many of the environments adolescents face are novel to them. As adolescents explore, their uncertainty about themselves and the world gradually decreases (Reiter et al., 2021; Romer et al., 2017), and thus specificity increases (temperature decreases) with learning (Ciranka and van den Bos, 2021). Findings suggest that adolescence might be a period of heightened learning sensitivity, coupled with reduced learning specificity. This can lead to increased learning when it does not involve decision-making, as in

Pavlovian learning, and – perhaps counterintuitively – decreased learning when it does involve decision-making, as in instrumental learning.

1.6 Adolescent Mental Health

Mental health disorders often have their onset in adolescence, with 14.5 years being the peak age of onset across all mental health conditions (Solmi et al., 2022). An estimated 50% of mental illnesses begin before age 14, with three-quarters occurring before age 25 (Rutter et al., 2006; Solmi et al., 2022). Global data indicate approximately one in seven adolescents is currently experiencing a mental health condition (Wasserman et al., 2005; WHO, 2024a,b), with rates having risen dramatically over the past decade (UNICEF, 2019). Interestingly, the *learning* processes outlined in the previous section provide a theoretical framework for understanding *why* adolescence might represent a period of vulnerability for the onset of mental illness.

1.6.1 Underlying Learning Processes

Learned associations can have robust influences on behaviour and mental health in both adaptive and maladaptive ways. Acquisition in Pavlovian learning can allow organisms to establish new reward/threat associations and engage in appropriate approach/avoidance behaviours. However, exaggerated Pavlovian learning can also play a role in the maintenance of unhealthy addictions, maladaptive anxiety responses and other mental health disorders (Chambers et al., 2003; Treanor et al., 2021). Differences in Pavlovian learning have been associated with mental health outcomes across development. Evidence of increased Pavlovian reward learning in adolescence has led researchers to propose that adolescence is a critical period of addiction vulnerability (Chambers et al., 2003), and addictive disorders commonly begin in adolescence (Strashny, 2016). Further, the synergy between social and drug rewards during this period might increase the potential for socially motivated substance abuse. Indeed, adolescents are more likely to use drugs and alcohol if those in their social group do (Strickland and Smith, 2014). Beyond addiction, reduced Pavlovian reward learning has also been associated with depression in adults and adolescents, and depressed individuals show blunted neural and behavioural responses to reward (O’Callaghan and Stringaris, 2019; Rappaport et al., 2020). In line with this, novel depression treatments, such as positive affect treatment, propose targeting reward learning by emphasising and encouraging learned associations between rewarding behaviours and positive mood (although this remains to be investigated in adolescents under age 18 years) (Craske et al., 2019).

Pavlovian threat learning is a key component in the development and maintenance of threat-related mental health conditions such as anxiety and phobias. The ability to extinguish and retain the extinction of a threat response is a crucial component of anxiety treatments such as exposure therapy (Raeder et al., 2020) in which individuals are helped to overcome anxiety through repeated exposure to feared scenarios. Although traditional methods of exposure therapy might be less effective for adolescents (particularly younger adolescents) than for adults (Huang et al., 2022; McGuire and Storch, 2019), harnessing the salience of social cues might have positive ramifications. For example, researchers have proposed using safety cues to increase tolerability and reduce attrition in the treatment of adolescent anxiety (Meyer et al., 2022). Although parents and caregivers might successfully serve as safety cues for children (Hostinar et al., 2015), a supportive friend might better help adolescents to effectively buffer stress (Calhoun et al., 2014; Sahi et al., 2021a). Considering experimental evidence regarding Pavlovian learning in adolescence might help clinicians to create a developmentally tailored treatment approach.

Computational psychiatry studies have shown that a variety of mental health problems, which often emerge in adolescence, are characterised by aberrant instrumental learning computations (Hauser et al., 2019). For example, in 18 – 25-year-olds, heightened punishment learning was associated with tighter coupling between neural signals and some computational measures (negative prediction errors) in individuals with higher levels of anxiety (Cavanagh et al., 2019). A recent meta-analysis also demonstrated that adults with depression or anxiety exhibit higher punishment and lower reward learning rates relative to adults without anxiety or depression (Pike and Robinson, 2022). Impaired learning from prediction errors has also been observed in other psychiatric disorders, including psychosis, alcohol abuse, and obsessive-compulsive disorder (Hauser et al., 2019). Although the majority of this research has been conducted with adults (Hauser et al., 2019), researchers have proposed that combining computational psychiatry and developmental neuroscience could inform our understanding of the cognitive processes and neural mechanisms that lead to mental health disorders in adolescence.

Research on adolescent neurodevelopment, particularly regarding learning processes, suggests that adolescence might represent a sensitive window during which stress can significantly impact mental health (Fuhrmann et al., 2015). Even before the COVID-19 pandemic, mental health challenges have constituted one of the leading cause of disability and poor life outcomes among young people (Erskine et al., 2015; Perou et al., 2013). Amidst growing concerns about adolescent mental health and their heightened vulnerability to stress and social disconnection, the pervasive role of social media might be a factor impacting adolescent development.

1.7 Adolescents and Social Media

The advent, rise and pervasive integration of social media into the daily lives of adolescents represent a profound shift in human social interactions, with implications for development (Nesi et al., 2018; Telzer and Maza, 2024). The digital transformation has provided unprecedented opportunities for social interaction, information access and self-expression, yet it has concurrently ignited considerable concern regarding the potential ramifications for adolescent mental health and wellbeing (Advisory, 2023; Orben et al., 2024; Telzer and Maza, 2024). The convergence of increased experiences of loneliness, protracted neurodevelopment, heightened environmental sensitivity and changes in cognitive processes (such as learning) during adolescence has generated substantial interest in understanding how social media might affect adolescent wellbeing. This intersection is particularly interesting as social disconnection has emerged as a public health concern despite unprecedented levels of digital connectivity. Paradoxically, whilst being one of the loneliest age groups, adolescents report more social media use than other age groups (Bayindir and Paisley, 2019). Amongst adolescents aged 13 – 17 years, 95% reported social media usage as of 2022, with over half indicating it would be difficult to give up (Vogels et al., 2022). Empirical evidence remains inconclusive regarding whether social media use alleviates or exacerbates loneliness (Nowland et al., 2018; Sahi et al., 2021b). Digital social interactions can enhance existing personal relationships and foster new, positive and supportive connections (Valkenburg and Peter, 2007). Some researchers propose a connection between digital social interactions and chronic loneliness (Kraut et al., 1998; Nie, 2001; Nowland et al., 2018), whilst others suggest digital social interactions might serve as a potential remedy for rising isolation (Alison Bryant et al., 2006; Nowland et al., 2018; Valkenburg and Peter, 2007). Indeed, some researchers propose that increasing loneliness among young people might be attributable to rising digital media use and the concomitant decline in in-person social interactions (Twenge et al., 2021, 2019).

The initial wave of research on this topic mostly focused on the broad metric of "time spent" on social media as a predictor of mental health outcomes, yielding largely inconclusive and inconsistent findings (Dienlin and Johannes, 2020; Maheux et al., 2025). This has led to a growing consensus within the field that conceptualising social media use as a monolithic entity is overly simplistic and fails to capture the complex ways in which adolescents interact with and are affected by these platforms (Maheux et al., 2025; Orben, 2020; Orben et al., 2024). As such, research is increasingly adopting more granular approaches, examining specific components of social media – including its content, features, functions and context – as well as considering the significant heterogeneity among adolescents in their patterns of use and susceptibility to its effects (Maheux et al., 2025, 2022; Valkenburg and Peter, 2013). Many early studies relied on

observational, cross-sectional designs, which inherently limit the ability to establish temporal precedence or causality. Longitudinal studies offer a more robust approach to disentangling the directional relationships between social media use and mental health trajectories (Achterberg et al., 2022; Coyne et al., 2020; Maza et al., 2023). The accuracy of self-reported measures of social media use have also been called into question. This has prompted a move towards incorporating more objective measures, such as data captured by smartphones or tracking applications (Parry et al., 2021; Reeves et al., 2021; Verbeij et al., 2021). Further, the rapidly changing nature of social media and user behaviours means that research methods must be continuously adapted to ensure they are relevant and valid (Bayer et al., 2020; Reeves et al., 2021).

Qualitative research can offer valuable insights into adolescents' lived experiences and perspectives on the impact of social media on their mental health and wellbeing. One study highlighted themes such as self-expression and validation sought through online platforms, the pervasive influence of appearance comparison and body ideals, the pressure to maintain constant connectivity, the potential for social engagement and peer support, and the risks associated with exposure to bullying and harmful content (Popat and Tarrant, 2023). Adolescents themselves seem to recognise the dual nature of social media, acknowledging both its potential benefits and its capacity to negatively affect their mental state. Their perspectives underscore the importance of focusing on the context and purpose of social media use.

Emerging findings underscore the importance of considering these more specific components of social media that might differentially impact adolescent development (Bayer et al., 2020; Maheux et al., 2025; Odgers and Jensen, 2020). For example, social networking features like direct messaging and public feeds can create meaningful opportunities for social support and belonging (Bayer et al., 2020; Dredge and Schreurs, 2020). Conversely, exposure to hateful or risky content, including self-harm imagery or pro-eating disorder content, can have detrimental effects on mental wellbeing (Allen et al., 2021; Barroso et al., 2023; Bayer et al., 2020; Crone and Konijn, 2018; Popat and Tarrant, 2023; Susi et al., 2023). Quantifiable feedback, such as "likes" and comments, can influence adolescents' sense of digital social status (Bayer et al., 2020; Lee et al., 2020; Telzer and Maza, 2024; Trekels et al., 2024). The asynchronous and potentially anonymous nature of online interactions can also exacerbate issues like cyberbullying, which has been consistently linked to poorer mental health outcomes (Hamm et al., 2015; K Kaye et al., 2020; Kwan et al., 2020; Marciano et al., 2020). Further, algorithm-driven content curated by AI might shape what information adolescents encounter and therefore how they compare themselves to others, raising important questions that deserve closer study (Nesi et al., 2018).

Beyond features, researchers are increasingly exploring underlying mechanisms at behavioural, cognitive and neurobiological levels that might help us understand how social media impacts adolescent mental health (Orben et al., 2024). For example, behaviourally, social media might influence self-presentation strategies, potentially leading to discrepancies between online and offline identities and impacting self-concept (Abeeel et al., 2017; Orben et al., 2024; Twomey and O'Reilly, 2017). The affordances of social media also facilitate social comparison processes, particularly concerning appearance and achievements, which can negatively affect self-esteem and body image (Choukas-Bradley et al., 2022; Hamm et al., 2015; Hawes et al., 2020; Popat and Tarrant, 2023). Cognitively, habitual social media checking may heighten responsiveness to social feedback and contribute to feelings of social exclusion or "fear of missing out" (K Kaye et al., 2020; Maza et al., 2023; Prinstein et al., 2020; Steele et al., 2020). Neuroimaging studies suggest that repeated exposure to digital social rewards can alter neural reactivity in brain regions associated with motivation, reward processing and cognitive control, potentially contributing to the development of habitual social media use patterns (Casey et al., 2008a; Maza et al., 2023).

There are also calls to acknowledge individual differences that might moderate the associations between social media use and mental health, recognising that the effects of social media on wellbeing likely differ from adolescent to adolescent (Beyens et al., 2020; Orben et al., 2022). These factors encompass a wide range of characteristics, including age, gender, marginalised status (e.g., LGBTQ+ youth, racial/ethnic minorities), neurobiological and social sensitivities and pre-existing mental health concerns (Achterberg et al., 2022; Allen et al., 2021; Hawes et al., 2020; Huang, 2022; Krause et al., 2021; Maheux et al., 2025; Tao and Fisher, 2022). For example, adolescents with heightened sensitivity to social feedback might experience more pronounced emotional responses to online interactions (Achterberg et al., 2022; Guyer et al., 2012; Maza et al., 2023; Rutherford et al., 2023). Neuroimaging studies have also pointed to individual differences. For example, one study found that individual differences in cortical thinning were related to heterogeneity in both social media use and wellbeing, albeit in different brain regions (Achterberg et al., 2022). Another longitudinal cohort study indicated that habitual social media checking behaviours in early adolescence might be associated with changes in the brain's sensitivity to social rewards and punishments (Maza et al., 2023). The controversial concept of problematic social media use, often characterised by excessive engagement, preoccupation and negative consequences, has emerged as an area of investigation (Huang, 2022). While not formally recognised as a clinical disorder, some researchers posit that problematic social media use shares similarities with behavioural addictions and has been associated with various mental health issues, including depression, anxiety and sleep disturbances (Beyens et al., 2020; Huang, 2022). Importantly, however, the

relationship between social media use (particularly problematic social media use) and mental health is likely bidirectional. A systematic review examining 1,747 papers on social media use, depression and anxiety found a significant and often reciprocal relationship (Lopes et al., 2022), meaning that while social media use was associated with changes in mental health over time, mental health was also associated with changes in social media use.

In conclusion, the relationship between social media and adolescent wellbeing is multifaceted and dynamic. While social media offers numerous opportunities for connection and growth, it also presents potential risks, particularly during this developmentally sensitive window. The existing body of research underscores the need to move beyond simplistic conceptualisations of screen time and to adopt more nuanced approaches that consider specific social media components, individual differences and underlying mechanisms of impact.

1.8 Thesis Overview

As described in this introduction, social disconnection is a growing global health threat with serious consequences for both physical and mental wellbeing. Adolescents are a particularly susceptible demographic, experiencing high and increasing rates of social isolation and loneliness despite increased digital connectivity. This vulnerability is underscored by the unique developmental characteristics of adolescence, a period defined by significant neurobiological changes and heightened sensitivity to social and affective experiences. Growing evidence suggests that adolescence might be a sensitive window of development, during which experiences like social isolation can exert an outsized and potentially lasting impact on brain and behaviour. In this context, the pervasive integration of social media into adolescent social life presents a complex challenge, as its impact on adolescent loneliness and wellbeing remains inconclusive. The aim of this thesis is to investigate social disconnection and digital social interactions in adolescents. More specifically, the research aims to advance understanding of how social isolation might impact adolescent mental health and highlight both the opportunities and limitations presented by digital social connections. This thesis ultimately addresses three overarching research questions, focusing on adolescents:

Research Questions

1. What are the effects of social disconnection?
2. Can digital social interactions remediate the effects of social disconnection?
3. How might social disconnection influence mental health and wellbeing?

Part one (chapters 2-4) describes an experimental study of social isolation in adolescents aged 16 – 19 years. This study sought to examine the psychological, cognitive and behavioural effects of acute (short-term) social isolation – both with and without digital social interactions – using a controlled, within-participant experimental design. This study also explored neural correlates of sensitivity to acute social isolation. **Chapter 2** investigates how acute social isolation affects both psychological state and threat learning in adolescents. Using self-report measures, this chapter first examines isolation-induced changes in state loneliness, boredom, social activity craving, state anxiety and mood. Additionally, it explores how isolation influences threat learning processes – specifically acquisition, extinction and retention – using both subjective ratings (arousal and valence) and objective physiological measurements (electrodermal activity) within a Pavlovian threat learning paradigm. Further, this study assesses whether these effects are modulated by digital social interactions, comparing psychological state and threat learning between sessions where adolescents experienced complete isolation versus sessions where they were permitted digital social interactions. This approach allows for assessment of both explicit and implicit threat responses following different types of social deprivation. **Chapter 3** investigates the effect of acute social isolation on adolescent reward responsiveness. Specifically, it examines the impact of isolation on both reward-seeking behaviour and reward learning processes. This chapter further explores whether the effects of isolation on reward responsiveness are modulated by access to digital social interactions. Additionally, it investigates potential domain-specificity by examining whether the effects of isolation differ for social versus nonsocial rewards. To address these questions, reward seeking was measured using an effort-based decision-making task, and reward learning was assessed via a reinforcement learning task. **Chapter 4** explores neural reward sensitivity as a predictor of acute social isolation-induced effects on reward responsiveness. It examines whether reward-related brain activity at baseline predicts the effects of isolation on reward seeking and reward learning. Participants underwent functional magnetic resonance imaging (fMRI) whilst completing a monetary incentive delay (MID) task. Neural reward sensitivity was quantified through both univariate and multivariate measures of activity in a priori selected regions of interest (ROIs). These neural measures were then correlated with behavioural measures of reward responsiveness following isolation.

Part two (chapters 5-7) uses non-experimental methods. **Chapter 5** explores the role of online and offline self-disclosure for adolescent (age 10 – 22 years) social connection. Given the increasing shift towards digital social interactions, this chapter presents a systematic review investigating the ways in which self-disclosure contributes to building social relationships and fulfilling social needs in adolescence, and comparing the effectiveness of online versus offline communication for this purpose. **Chapter 6** focuses on loneliness and digital social interactions

among late adolescents (aged 18 – 25 years) during the COVID-19 pandemic. This chapter presents data from an observational COVID study investigating digital social engagement, objective social isolation, psychological wellbeing and social needs within late adolescents amid early pandemic restrictions. This chapter examines whether the frequency of digital social interactions was associated with self-reported loneliness, happiness and depressive symptoms in order to explore whether technology-mediated social contact served protective functions for late adolescents during a period of unprecedented social (physical) distancing. **Chapter 7** presents data from the COVID study, focusing on the impact of the COVID-19 pandemic on emerging adults (aged 18 – 29 years) using a mixed-methods approach, exploring the emotional experiences during the immediate onset of the pandemic. Further, this chapter mapped these emotional experiences to self-reported changes in mental health. By combining qualitative analysis of personal narratives with quantitative mental health measures, the aim was to provide a nuanced understanding of pandemic experiences and challenges among emerging adults during this naturally occurring period of increased social disconnection. Finally, **Chapter 8** synthesises the empirical findings from this thesis and evaluates their theoretical implications, contributions and applications within science and society.

Part I

Chapter 2

The Effects of Social Isolation on Adolescent Threat Learning

A version of this chapter has been published:

Towner, E., Thomas, K., Tomova, L., & Blakemore, S.-J. (2024). Increased threat learning after social isolation in human adolescents. *Royal Society Open Science*, 11(11), 240101.
DOI: 10.1098/rsos.240101

2.1 Introduction

As described in the introduction, adolescence is a period of emotional and social sensitivity. Today, adolescents also report high levels of loneliness and social disconnection and heavy social media use. With mental health conditions increasing in prevalence and severity, many have expressed that we are currently in a youth mental health crisis. Given that adolescence is also a period of heightened neuroplasticity and a time of social reorientation, adolescence might constitute a sensitive period for the effects of isolation on mental health. Loneliness during adolescence might have outsized, negative and long-lasting consequences for wellbeing.

Of particular interest is the link between loneliness and anxiety. Anxiety can be conceptualised as a future-oriented state triggered by prospective threat (Mobbs, 2018). Associative learning mechanisms, in which individuals learn to associate threats with otherwise neutral cues, are proposed to be crucial mechanisms in the aetiology of anxiety disorders (Pittig et al., 2018). The Evolutionary Theory of Loneliness (Cacioppo and Cacioppo, 2018) provides an explanation as to why loneliness might be linked with heightened responses to threat (Hawkley and Cacioppo, 2011). This theory suggests that social isolation induces an adverse biological

signal (loneliness), which evolved to promote vigilance against danger (such as threats of predation or lack of resources; Cacioppo and Cacioppo, 2018; Cacioppo et al., 2016). This loneliness-induced anxiety might thereby increase survival prospects by increasing threat vigilance.

As mentioned in Section 1.3.3, in animal models social isolation has been shown to increase threat responding (reactivity to potentially threatening events) demonstrated by increased anxiety-like behaviours in rodents (particularly when isolation occurs during development; Grigoryan et al., 2022; Lukkes et al., 2009a). In addition to threat responding, animal research also suggests that isolation can impact threat *learning*. For example, social isolation results in increased conditioned threat responses in rodents (Lukkes et al., 2009a; Matsuda et al., 2018). Rodents that were socially isolated in adolescence displayed both reduced vicarious threat learning and greater direct threat learning compared to socially housed mice (Panksepp and Lahvis, 2016; Yusufshaq and Rosenkranz, 2013). Further, socially isolated adolescent (Skelly et al., 2015) and adult (Wisłowska-Stanek et al., 2022) rodents exhibit impaired threat extinction learning compared to socially housed conspecifics.

In humans, both chronic and state loneliness have been associated with altered threat processing, with studies finding links between loneliness and threat hypervigilance, particularly towards social threats, at the neural, behavioural and self-report level (Cacioppo et al., 2015; D'Agostino et al., 2019; Wei et al., 2020). Research investigating human Pavlovian threat learning has shown that young adults with high levels of chronic loneliness had a higher tendency for fear relapse, or the return of a threat response after extinction (as measured by electrodermal activity) compared to individuals with low levels of chronic loneliness (Hornstein and Eisenberger, 2022). Another study found that men (average age 26 years) reporting high levels of chronic loneliness displayed hyperreactivity in the amygdala (a brain region associated with emotional responses including fear and anxiety; LeDoux, 2007) during fear conditioning compared to men reporting low levels of loneliness (Morr et al., 2022). Further, high-chronic-lonely men showed reduced amygdala habituation during repeated exposure to fearful faces (Morr et al., 2022), though this pattern was not found in women. Further, social support can act as a safety signal, reducing fear learning and enhancing fear extinction (Hornstein and Eisenberger, 2018). Unlike the animal literature, in humans there is a lack of experimental studies which directly manipulate social isolation and enable inferences that go beyond correlations between self-reported loneliness and threat learning. Experimental studies in humans can also elucidate whether there are different effects of social isolation on threat learning when participants are physically isolated but have access to digital social interactions.

2.1.1 Aims

In this chapter, the effect of acute isolation on psychological state and threat learning in human adolescents aged 16 – 19 years is investigated, both with and without digital social interactions. Participants underwent three sessions, starting with baseline and followed by two isolation sessions of up to four hours. One isolation session (iso-total) involved isolation from all social interactions, while the other (iso-with-media) allowed for digital social interactions only. At each session (baseline, iso-total and iso-with-media), psychological state was measured via self-report and threat learning was measured using self-report ratings (arousal and valence) and physiological measurements (electrodermal activity) during a Pavlovian threat learning paradigm. Here, I focus on three research questions: (Q1) How does acute isolation impact psychological state (including loneliness, social activity craving, boredom and mood)?; (Q2) How does acute isolation impact threat learning (including acquisition, extinction and retention)?; and (Q3) Do digital social interactions alter the effects of acute isolation on psychological state and threat learning? It was hypothesised that isolation would increase loneliness, negative mood, social activity craving and anxiety, while decreasing positive mood. Further, it was hypothesised that isolation would heighten threat learning by increasing threat acquisition, decreasing threat extinction and increasing threat retention. Finally, it was hypothesised that digital social interactions might lessen the effects of isolation on both psychological state and threat learning.

2.2 Methods

2.2.1 Study Design

In this social isolation study, an experimental approach was employed to investigate the effects of acute isolation, with and without digital social interactions, on cognition in human adolescents aged 16 – 19 years. This study aimed to test the effects of isolation in a population for whom the consequences of loneliness are particularly important (Hammond et al., 2019; Tomova et al., 2021). This study was preregistered¹ on the Open Science Framework.

2.2.2 Participants

Prior to preregistration, a power analysis for the experimental manipulation (the ability for acute social isolation to induce feelings of loneliness) was conducted using pilot data (a subset of data from Tomova et al., 2020 involving 18 – 24 year olds). In this pilot data,

¹DOI: 10.17605/osf.io/kbgsv

short-term isolation affected feelings of loneliness (using a self-report loneliness scale ranging from 0 – 100) with an effect size (Cohen's d) of 0.47. The power analysis showed that 38 participants were required to detect this medium effect size to achieve a power of .80 ($1 - \beta$) at an alpha of .05.

Forty-two participants were enrolled; 2 participants were unable to complete all experimental sessions. Therefore, this study included 40 participants ($M_{age} = 17.1$, $SD_{age} = 0.9$, $Range_{age} = 16 - 19$ years, 22 female). In order to increase the power to detect effects related to the experimental manipulation (social isolation), potential variation due to age-related differences was minimised by restricting the age range of participants to 16 – 19 years. Participants were recruited through advertisements (flyers and online) and local schools in Cambridge. The study description indicated that the research was interested in studying how different forms of spending time alone (with or without access to digital interactions) affects adolescent cognition. Potential participants were first assessed for eligibility via a screening questionnaire (administered through Qualtrics and REDCap; see the supplement for details on software). Participants were asked to indicate their sex and their gender (how they describe themselves). In the sample of participants, sex labels were not different from gender labels and the term sex is used throughout.

To be deemed eligible, candidates had to be between 16 – 19 years of age, with no history of brain damage, no currently diagnosed mental health disorders, and no metal implants in their body (as this study was part of a larger project involving an MRI scan). The study was conducted amidst the COVID-19 pandemic, hence a COVID-19 risk assessment formed a part of the exclusion criteria, disqualifying candidates with chronic illnesses (such as asthma), current health issues (or a positive COVID-19 test) and those who smoked. The conflation of effects of chronic and acute isolation and loneliness was avoided for experimental reasons and also to avoid exposing vulnerable individuals to isolation. Therefore, candidates living alone, those who recorded high chronic loneliness levels on the UCLA loneliness scale (Russell, 1996; a score > 50 was regarded as high, one standard deviation above an adolescent sample mean) and/or those with significantly smaller social network sizes as compared to a previous adolescent sample (Von Der Heide et al., 2014; $n = 40$), were excluded. Social network size was estimated by the number of close friends and number of social interactions over the previous month, considering both in-person and digital social interactions of a non-professional nature. Given the social distancing norms during the pandemic, the study set lower exclusion thresholds for social network size than used previously (Tomova et al., 2020). Candidates reporting fewer than two close friends and/or 10 social interactions within the last month (approximately seven standard deviations below the adolescent mean; Von Der Heide et al., 2014) were excluded. This resulted in a sample of participants who were socially well-connected in that they reported

having frequent social interactions (number of face-to-face or digital interactions that were primarily social in nature in the past month ($M = 36$, $SD = 32.2$, $\text{Min} = 10$) and several close relationships ($M = 7.6$, $SD = 4.2$, $\text{Min} = 2$). Participants reported average levels of pre-existing chronic loneliness (as measured by the UCLA loneliness scale) for their age group ($M = 35.6$, $SD = 6.2$; Lasgaard 2007; Russell 1996).

The Psychology Research Ethics Committee at the University of Cambridge, reviewed the experimental procedures. Prior to the study, participants (and parents of participants under 18) provided informed consent. For their involvement in three sessions, participants were compensated between £107 and £127, depending on task performance.

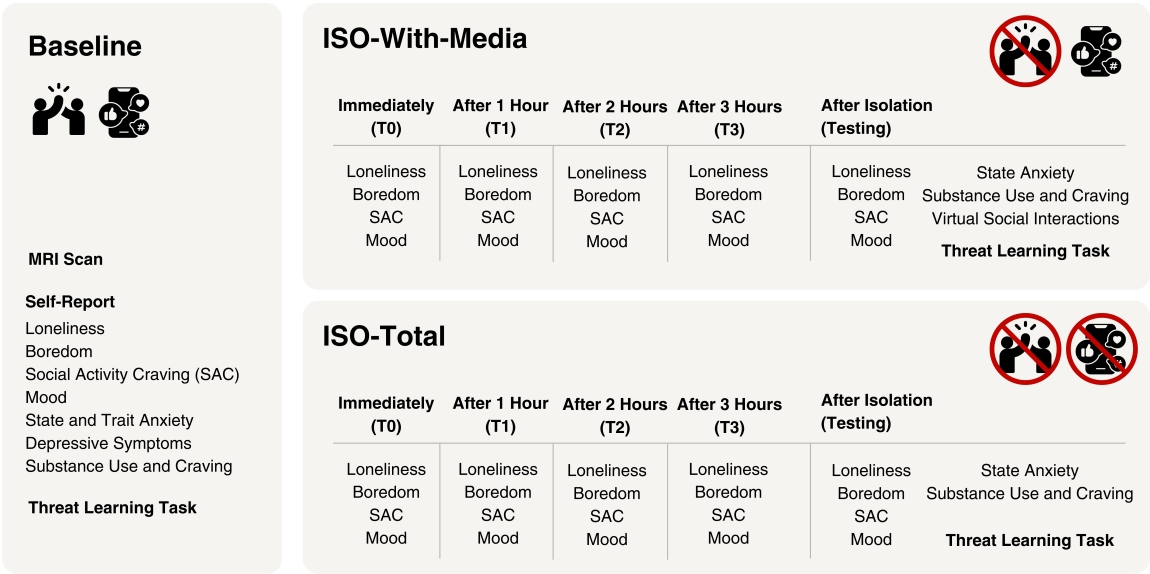
2.2.3 Procedures

Participants took part in three experimental sessions (baseline, iso-with-media and iso-total; Figure 2.1). Each session was separated by a minimum of 24 hours (days between sessions ranged from 2 – 125 [$M = 32.5$, $SD = 27.51$] across participants). The first session was a baseline, consisting of neuroimaging (described in subsequent chapters) and testing (which included tasks, questionnaires, and physiological measurements). After baseline, participants returned for two sessions of isolation (order counterbalanced between participants) followed by testing (testing took place in the same room as isolation and began immediately following the isolation period). All participants underwent all three experimental conditions. The sequence of conditions was pseudo-randomly assigned per participant, with the baseline always being the first and with each sequence having approximately the same likelihood in the full sample. This design allowed for an analysis of the effects of both forms of isolation, using a baseline that had not been influenced by any previous isolation experience. It also enabled a direct comparison between the effects of complete isolation and isolation with access to digital interactions.

2.2.3.1 Social Isolation

Following the methods of the study in adults by Tomova et al. (2020), this study aimed to induce a temporary subjective sense of state loneliness among adolescent participants. An experimental manipulation of social isolation under different conditions was conducted across two separate sessions. One session involved up to four hours of complete social isolation (iso-total), where participants had no access to any form of social interaction. The other session involved up to four hours of social isolation, with access only to digital social interactions (iso-with-media). Two hours of isolation was sufficient to increase self-reported state loneliness in adolescents according to piloting and reanalysis of a subset of data from Tomova et al. (2020; 18 – 24 year old participants). The duration of isolation was therefore reduced compared with

Figure 2.1 Social Isolation Study Design



Note. This figure illustrates the social isolation study design, including the components of the procedures relevant to this manuscript that were delivered at each session. A within-participant design was used and the isolation sessions were counterbalanced between participants. The self-report questionnaires collected at each hour of isolation and at the beginning of testing are listed. For more information on the measures used, see the "Questionnaire" section below. The threat learning task was administered at each session. Further details on the other behavioural tasks and the MRI scan administered in this study are described in subsequent chapters and elsewhere (Tomova et al., 2025). Source: Reproduced from Towner, E., Thomas, K., Tomova, L., & Blakemore, S.-J. (2024). Royal Society Open Science. CC-BY 4.0.

Tomova et al. (2020; experiment conducted with adult participants). In the current study, each isolation session lasted a minimum of 3 hours and 30 mins. An additional 0 – 30 mins of isolation, in five-minute increments, was randomly assigned to each session. This was done to prevent participants from being able to predict the end of their isolation in either session. Therefore, all sessions lasted between 3 hours and 30 mins and 4 hours. The average isolation duration was similar across sessions (iso-with-media: $M = 3$ hours 47 mins, $SD = 10$ mins; iso-total: $M = 3$ hours 46 mins, $SD = 11.20$ mins; $t(39) = 0.30$, $p = .765$).

Participants could spend the isolation period as desired (excluding sleeping). The isolation room contained an armchair, desk, office chair, desktop computer, physiological hardware, fridge with food and beverages and nonsocial materials (puzzles, sudoku books, digital and analogue games). The room had a roof window, which allowed day light to enter the room but kept participants from seeing other people outside the building. Participants could also bring their own nonsocial items (crafts, textbooks, writing materials). Participants brought homework,

art materials, nail polish and a jewellery making kit, for example. For the iso-with-media session, materials with social components (music, novels) were also allowed and participants retained their electronic devices and had internet access. Most participants brought their tablet or laptop as well as their phones. In the iso-total session, participants were not allowed to bring their own electronic devices, but retained access to a messaging application (Slack; in case of emergency) and the experimental software via a desktop computer. Participants received a detailed PDF of instructions and they completed digital questionnaires hourly on the provided desktop computer (reminders were set via an analogue alarm clock). During isolation and subsequent testing, a live camera feed (without audio) allowed a researcher to periodically monitor participants. Participants were informed about the camera in an information sheet they received before agreeing to participate in the experiment. After the session, a member of the research team chatted with the participants about their experiences during isolation and made sure participants were not feeling troubled. Data collection and analysis were not performed blind to the conditions of the experiment.

2.2.4 Measures

2.2.4.1 Questionnaires

Psychological State. At the start of testing in each of the three sessions (baseline, iso-with-media, iso-total), self-reported data was gathered on state loneliness, social activity craving (i.e., how much participants wanted to engage in a social activity), boredom and mood (evaluated with the Positive and Negative Affect Schedule; PANAS; Watson et al., 1988). At baseline only, data was also collected on trait anxiety (using the trait subscale of the STAI; Spielberger, 1983) and depression (utilising the Center for Epidemiological Studies Depression [CES-D] scale; Radloff, 1977). In both the iso-total and iso-with-media sessions, state loneliness, social activity craving, boredom and mood were also evaluated at hourly intervals during the session. State anxiety was collected once in all three sessions (at the start of testing) using the state subscale of the State Trait Anxiety Index (STAI; Spielberger, 1983).

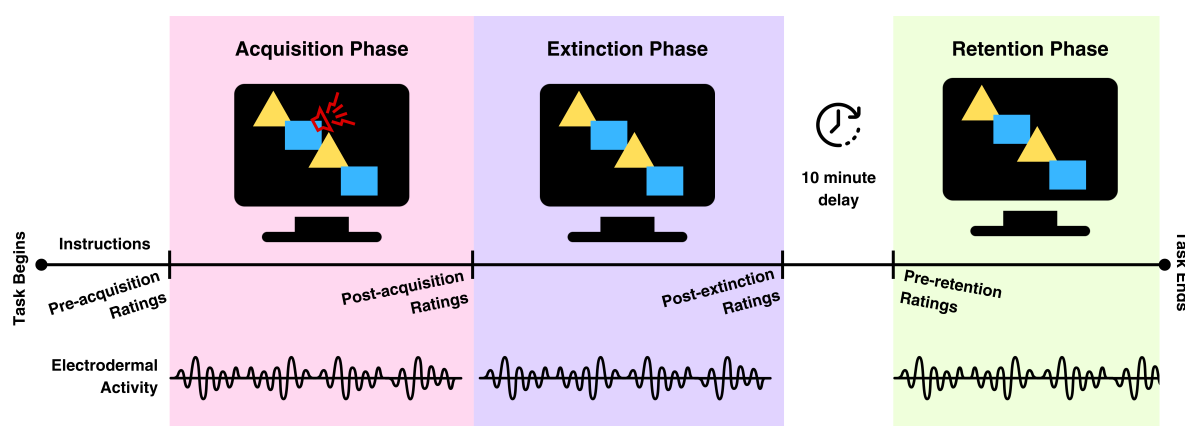
Digital Social Interactions. Participants completed a questionnaire about their digital social interactions during the isolation period after the iso-with-media session. They estimated the percentage of time they spent engaging in digital social interactions during the session (ranging from 0 – 100%). Participants were also asked to specify the primary digital social interaction method(s) (e.g., texting/messaging, voice calls, video calls, commenting/posting, gaming, other) and platform(s) (e.g., Instagram, Facebook, Facebook Messenger, Snapchat, TikTok, Twitter, WhatsApp, other) they used during the session. Additionally, participants identified

their digital interaction partners (e.g., friends, family, acquaintances, romantic partners, other). Participants could select multiple options and, if they selected "other", were asked to elaborate.

2.2.4.2 Threat Learning Task

During testing in each of the three sessions (baseline, iso-with-media and iso-total), threat learning was measured using a Pavlovian threat learning paradigm (programmed using PsychoPy) in which participants learned to associate neutral shapes with an aversive sound (a metal screech). Threat responses were measured via self-report ratings and physiologically via electrodermal activity across three phases (acquisition, extinction and retention)(Figure 2.2). Pre-acquisition responses were also collected for self-report ratings. One shape (such as a blue rectangle) served as a threat cue (CS+) and another (such as a yellow triangle) as a safety cue (CS-). There were six shape stimuli in total which were fully counterbalanced between participants and sessions, with participants seeing a different pair of shape stimuli in each session (to avoid carryover effects).

Figure 2.2 Threat Learning Task



Note. This figure illustrates the critical phases of the threat learning task. Participants provided self-report ratings (valence and arousal) at each tick mark on the timeline. Electrodermal activity was recorded continuously throughout the three phases. During acquisition, participants learned that one of two neutral shapes (threat cue) was sometimes paired with an aversive sound. During extinction, participants learned that the threat cue was no longer paired with the aversive sound. After a 10-min delay (that included an unrelated task), participants again saw the cues with no aversive sound (retention). *Source: Reproduced from Towner, E., Thomas, K., Tomova, L., & Blakemore, S.-J. (2024). Royal Society Open Science. CC-BY 4.0.*

In the baseline session, each participant first underwent a sound calibration: the aversive sound was initially played to each participant through headphones. Participants were given the opportunity to change the volume to make the sound "unpleasant, but not painful" and

this volume was recorded and used in all subsequent sessions. The researcher then explained to the participant how to attach electrodes to their left middle and index finger to measure electrodermal activity and start the recording and task presentation software. The researcher monitored the application and execution of this procedure. This meant that participants could set up electrodermal activity recordings and self-administer the task independently at the following isolation sessions. Written instructions were also provided at each session. A Biopac (MP36R) recording system together with AcqKnowledge software was used to amplify and record electrodermal activity (electrodermal activity channel sample rate [2000 samples/second]; acquisition sampling rate [2000 samples/second]; gain [x2000]; Braithwaite et al., 2013). A Biopac electrodermal activity finger transducer (SS3LA) with isotonic gel (GEL101) was used.

Pre-Acquisition Ratings. Once the task began, participants were given instructions via a computer monitor. First, they were shown the two shapes (threat and safety cues) and asked to judge the valence and arousal of each shape (pre-acquisition ratings). For valence, participants were asked "How unpleasant/pleasant do you find this shape?" (from [1] very unpleasant to [9] very pleasant). For arousal, participants were asked "How anxious does this shape (or sound) make you feel?" (from [1] not anxious to [9] very anxious). Rating scale tick marks were accompanied by figures from the Self-Assessment Manikin (Bradley and Lang, 1994), and a pictographic scale was used to assess affective responses on dimensions of valence and arousal. There was no time restriction for participant ratings.

Acquisition Phase. After pre-acquisition ratings, participants completed an acquisition (i.e., learning) phase. Participants were told they would see different coloured shapes, and that some of the shapes might be followed by a sound. There were 24 trials in which a shape (either the threat or safety cue) was presented on the screen for 2 s (with a 7 s inter-trial interval). On 50% of threat cue trials, the shape co-terminated with the aversive sound for the last 500 ms of that trial (16 threat cue trials total; 8 paired with aversive sound and 8 without). The safety cue (8 trials) was never accompanied by the aversive sound. Participants were not informed which shape would be followed by the sound. They were told that, after some time, a grey dot would appear in the centre of the shape, and to press the spacebar with their right hand as quickly as possible upon seeing the grey dot. This dot appeared after 1.5 s on each trial and served as an attention check. Immediately after the acquisition phase, participants again rated the valence and arousal of both shapes. As a second attention check at the end of the acquisition phase, participants were then asked to indicate which shape was followed by the sound. Data were not excluded from the analysis based on either attention check, but post-hoc sensitivity analyses

concluded that excluding data based on these attention checks did not change the overall pattern of results (see the supplement).

Extinction Phase. Extinction measures the ability to suppress previously learned threat associations once they are no longer predictive of threat. Therefore, during the extinction phase the aversive sound was no longer paired with either stimulus. Participants were shown identical instructions as in the acquisition phase. The extinction phase consisted of 16 trials (8 threat cues; 8 safety cues). After extinction, participants again rated the valence and arousal of both shapes.

Retention Phase. After a 10-min delay, during which participants completed an unrelated social influence task (Knoll et al., 2017, 2015), retention was assessed. In the retention phase, the threat response was measured after a period of time had elapsed in order to assess long-term threat responding. Participants were shown identical instructions as in the acquisition and extinction phases. Participants rated the valence and arousal of both shapes then underwent 16 trials (8 threat cues [no longer paired with the aversive sound], 8 safety cues).

Unconditioned Stimulus Ratings. At the end of the task, participants were asked to rate the aversive sound (US) in arousal and valence.

Design Considerations. In order to avoid problems with concentration or fatigue, the task was kept as short as possible while still following design recommendations (Ryan et al., 2019; Shechner et al., 2015). To reduce the probability that participants would deduce the structure of the task (repeated at baseline, iso-with-media and iso-total), a number of trials were included before the extinction phase began and after the retention phase had ended in which the threat cue was paired with the aversive sound. However, these trials were not included in the analyses – and their placements (at the beginning of the extinction phase and at the end of the retention phase) were chosen to avoid contamination with other phases. For full information regarding the task design, see the supplement.

2.2.4.3 Other Tasks

During testing in each of the three sessions (baseline, iso-with-media and iso-total) participants also completed several other tasks, including a reward seeking task (effort based decision making), reward learning task (reinforcement learning), a cognitive control task (go/no-go) and a social influence task. The acquisition and extinction phase of the threat learning task were completed after the reward seeking task, the reward learning task and the cognitive control task

(which were counterbalanced between participants). Participants completed the social influence task between the extinction and retention phase of the threat learning task, as described above. Findings from other tasks (reward seeking, reward learning, social influence, cognitive control) are reported in subsequent chapters and elsewhere.

2.2.5 Data Analysis

2.2.5.1 Psychological State

Analyses of the effects of isolation on participants' psychological state are first reported. For these analyses, linear mixed effects models were used to estimate the fixed effect of session on each state variable. "Participant" was included as a random effect, allowing intercepts to vary between participants. For state variables that were collected hourly during the isolation sessions (state loneliness, boredom, social activity craving, positive mood and negative mood), ratings at hour 3 were used as the ultimate measure of experimentally-induced psychological state, as this captured participants' affective state after a substantial period of isolation but before we told them the isolation period was over. For state variables collected once (state anxiety), ratings at the final hour (just before the experimental tasks) were used. The formula for this model is displayed in Equation 2.1. ANOVA tests of fixed effects of session were performed on each model. Session effects were interpreted using post-hoc pairwise comparisons of the contrasts between sessions using estimated marginal means. Post-hoc pairwise comparisons were corrected using the Bonferroni method for multiple comparisons (three sessions – baseline, iso-total and iso-with-media) for an adjusted alpha level of .016 (.05/3).

$$variable_{state} = session + (1|participant) \quad (2.1)$$

Hourly Trends. For loneliness, boredom, social activity craving, positive mood and negative mood, hourly linear trends were also estimated for both isolation sessions and compared to test for differences between sessions. For each hourly state variable, linear mixed effects models were used to estimate the fixed effects of session, hour and the interaction between session and hour. For these analyses, random effects were specified using a maximal structure for participant (the formula for this model is displayed in Equation 2.2), which estimates random intercepts and random slopes for session, hour and the session by hour interaction, along with all correlations among these random effects. To address convergence issues common with maximal random effects structures, the model was fit using the bobyqa optimizer. ANOVA tests of fixed effects were performed to evaluate the significance of session, hour, and their interaction. Post-hoc comparisons of hourly trends between sessions were conducted using

estimated marginal trends, which calculates the slope of change per hour for each isolation condition and tests whether these slopes significantly differ. These analyses were restricted to the isolation sessions (iso-total and iso-with-media) as baseline sessions did not include hourly measurements. Each hourly psychological state variable was analysed separately. State anxiety was excluded because it was only measured once per session. Post-hoc pairwise comparisons were corrected using the Bonferroni method for multiple comparisons (two sessions – iso-total and iso-with-media) for an adjusted alpha level of .025 (.05/2).

$$variable_{state} = session \times hour + (session \times hour | participant) \quad (2.2)$$

2.2.5.2 Threat Learning

To compare differences in threat responses associated with the experimental manipulation, linear mixed effects models were used. Linear mixed effects models were used due to the within-participant structure of the data (data were nested within participants). Effects of interest were estimated as the fixed effect of the interaction between session (baseline, iso-with-media and iso-total), phase (pre-acquisition, acquisition, extinction, and retention) and cue (threat and safety) on each response (arousal, valence and electrodermal activity²). "Participant" was included as a random effect, allowing intercepts to vary between participants (accounting for individual variation in participants' average responses). Random slopes were not included in the models due to the mixed factorial design (in designs with a single observation per unit per cell, random slope variance cannot be distinguished from random error variance and thus random slopes should not be included; Barr, 2013). The formula for these models is displayed in Equation 2.3. ANOVA tests of fixed effects of the categorical predictors and interactions were performed on each model. Interactions were interpreted using post-hoc pairwise comparisons of the contrasts between threat responding (responses to the threat and safety cue at each session and phase) and threat discrimination (the difference in response between the threat and safety cue at each session and phase) using estimated marginal means and errors. Post-hoc pairwise comparisons were corrected using the Bonferroni method for multiple comparisons (three sessions – baseline, iso-total and iso-with-media; three responses – arousal ratings, valence ratings and electrodermal activity) for an adjusted alpha level of .005 (.05/9). These models allowed threat learning to be assessed across phases of the task as well as to compare sessions (to determine whether digital social interactions remediated the effects of isolation on threat learning). Confirmatory analyses were carried out using R.

$$response = session \times phase \times cue + (1 | participant) \quad (2.3)$$

²There was no pre-acquisition phase for electrodermal activity.

Regarding the statistical power for the threat learning analyses, no previous study had examined the effects of experimental isolation on threat learning in human adolescents from which effect-size estimates could have been based. Importantly, however, a within-participant design was utilised (where each factor in the 3-way interaction was also a within-participant factor). This type of within-participant design requires only one third of the number of participants as a between-participants design to achieve similar statistical power (Lakens and Caldwell, 2021).

Electrodermal Activity Preprocessing. Electrodermal activity data were preprocessed using standard parameters in NeuroKit2 (Makowski et al., 2021). This involved removing noise and smoothing the signal (using a low-pass filter with a 5 Hz cutoff frequency and a 4th order Butterworth filter) before decomposing the signal into phasic and tonic components (by passing the cleaned data through a high-pass filter with a cutoff frequency of 0.05 Hz). After preprocessing, both the processed and raw electrodermal activity data were visually inspected by one rater for quality control. The quality of the data was good and no participants or trials were removed from the data. Epochs were identified using event markers for each condition. Peaks were identified in the phasic component of the processed electrodermal activity signal using the default neurokit settings. Responding during threat learning is, by definition, temporally dynamic (Lonsdorf et al., 2017; Wen et al., 2022). Therefore, electrodermal activity (peak amplitude) was averaged per condition (i.e., threat, safety) for the last half of the acquisition and extinction phase (once learning occurred), and first half of the retention phase (before additional extinction occurred) in order to capture the relevant response of interest. These time bins were preregistered and selected based on prior literature (Ryan et al., 2019). In order to separate the learned response from the response to the aversive sound itself, threat trials paired with the aversive sound were excluded from analyses of electrodermal activity.

2.2.5.3 Mechanisms

In this chapter, the degree to which participants' psychological state during isolation (state loneliness, boredom, social activity craving, positive and negative mood and state anxiety) act as "mechanisms" (as defined in Montoya and Hayes, 2017) by which isolation affects threat learning was sought to be explored. Causal processes are typically complex, involving various underlying mechanisms. Several processes might simultaneously mediate or "carry" the effect of isolation on threat learning. Parallel mediation models respect such complexities and allow for the comparison of the size of indirect effects through different mediators. To quantify the degree to which the six state variables act as "mechanisms" by which isolation affects threat learning, a path-analytic framework was employed to perform a two-condition

within-participant statistical parallel mediation analysis between the iso-total and iso-with-media sessions (Montoya and Hayes, 2017). Two conditions (iso-total and iso-with-media) were included in these analyses (baseline was not). This was because the order of the two isolation sessions was counterbalanced between participants and identical in procedure apart from the experimental manipulation (whether participants were allowed access to digital social interactions or not). In contrast, the baseline session was always conducted first and did not include an experimental manipulation.

The MEMORE macro (Montoya and Hayes, 2017) in SPSS was used to estimate parallel multiple mediation between the two isolation sessions and threat learning (separately for each phase and cue [including the threat cue, safety cue, and difference between the two – threat discrimination]). Each state variable was entered as a mediator simultaneously (state loneliness, boredom, social activity craving, positive mood, negative mood, and state anxiety). Corresponding to the psychological state analyses above, for state variables that were collected hourly (state loneliness, boredom, social activity craving, positive mood and negative mood), ratings at hour 3 were used as the ultimate measure of experimentally-induced psychological state. For state variables collected once (state anxiety), ratings at the final hour (just before the experimental tasks) were used. Estimates of the indirect effects (i.e., how much isolation influenced threat learning through each state variable) were focused on. Standard errors and p-values of the indirect effects were not derived as the sampling distribution of indirect effects is not typically normal (Bollen and Stine, 1990; Stone and Sobel, 1990). Instead, 95% confidence intervals were constructed using the percentile bootstrap method with 10,000 bootstrap samples (Montoya and Hayes, 2017). Confidence intervals that did not overlap with zero were interpreted as meaningful (Montoya and Hayes, 2017). By using parallel mediation, the indirect effect of each state variable was able to be estimated while simultaneously controlling for other state variables (i.e., the effects are not confounded with the effects of other state variables).

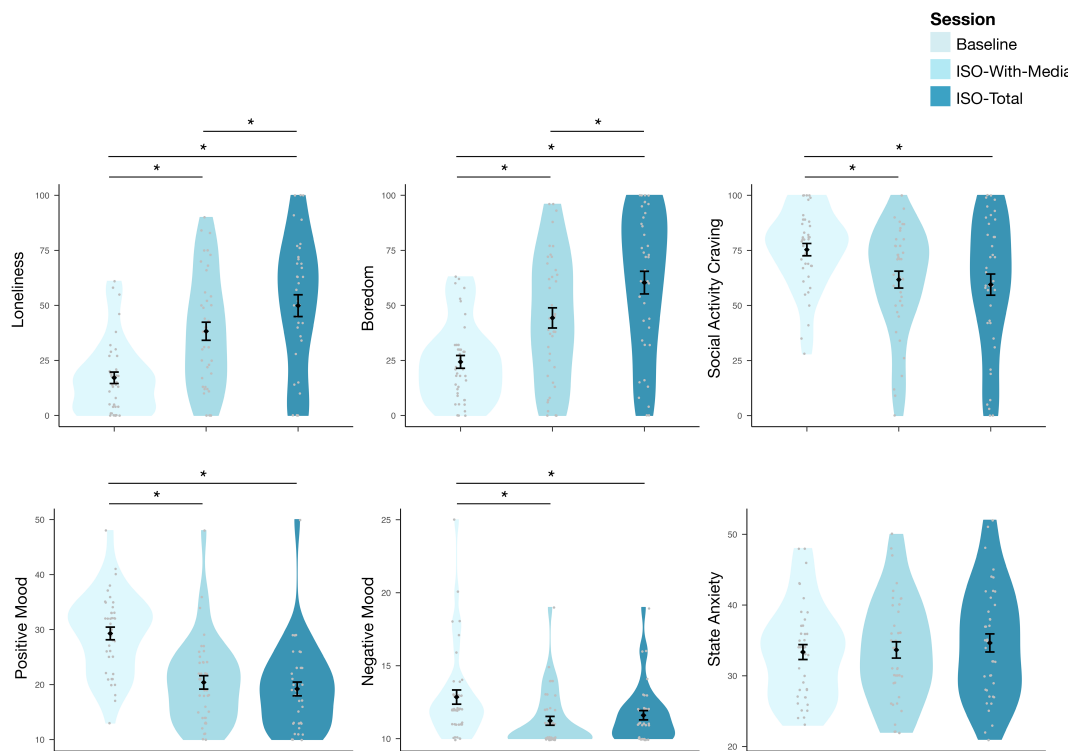
2.3 Results

2.3.1 Psychological State

For loneliness ($F(2, 78) = 26.03, p < .001$), boredom ($F(2, 77) = 28.24, p < .001$), social activity craving ($F(2, 77) = 13.34, p < .001$), positive mood ($F(2, 76) = 51.30, p < .001$) and negative mood ($F(2, 77) = 7.67, p = .001$), there was an effect of session (Figure 2.3). There was no effect of session on state anxiety ($F(2, 77) = 0.40, p = .670$). Post-hoc comparisons showed that after a period of isolation, participants reported higher levels of loneliness and boredom and lower levels of positive mood, negative mood and social activity craving at

both isolation sessions compared to the baseline session (Figure 2.3). Further, loneliness and boredom were elevated after the iso-total compared to the iso-with-media session. There were no differences between any of the sessions for state anxiety. State variable measurements were taken just prior to testing at the baseline session and after a period of isolation for the iso-with-media and iso-total sessions. For full results, see the supplement.

Figure 2.3 Psychological State



Note. The effects of isolation on participants' psychological state (state loneliness, boredom, social activity craving, positive and negative mood and state anxiety). Points indicate individual participant responses, violins show the estimated data distributions, diamonds represent the estimated marginal means, and bars indicate standard errors around the estimated marginal means. Lines (with stars) indicate a significant difference in post-hoc pairwise comparisons of estimated marginal means (Bonferroni corrected for multiple comparisons [adjusted alpha = .016])(See the supplement for the full list of post-hoc comparisons). *Source:* Reproduced from Towner, E., Thomas, K., Tomova, L., & Blakemore, S.-J. (2024). *Royal Society Open Science*. CC-BY 4.0.

2.3.1.1 Hourly Trends

When considering psychological state at each hour of the isolation period (Figure 2.4), for loneliness there was a two-way interaction between hour and session ($F(1, 39.17) =$

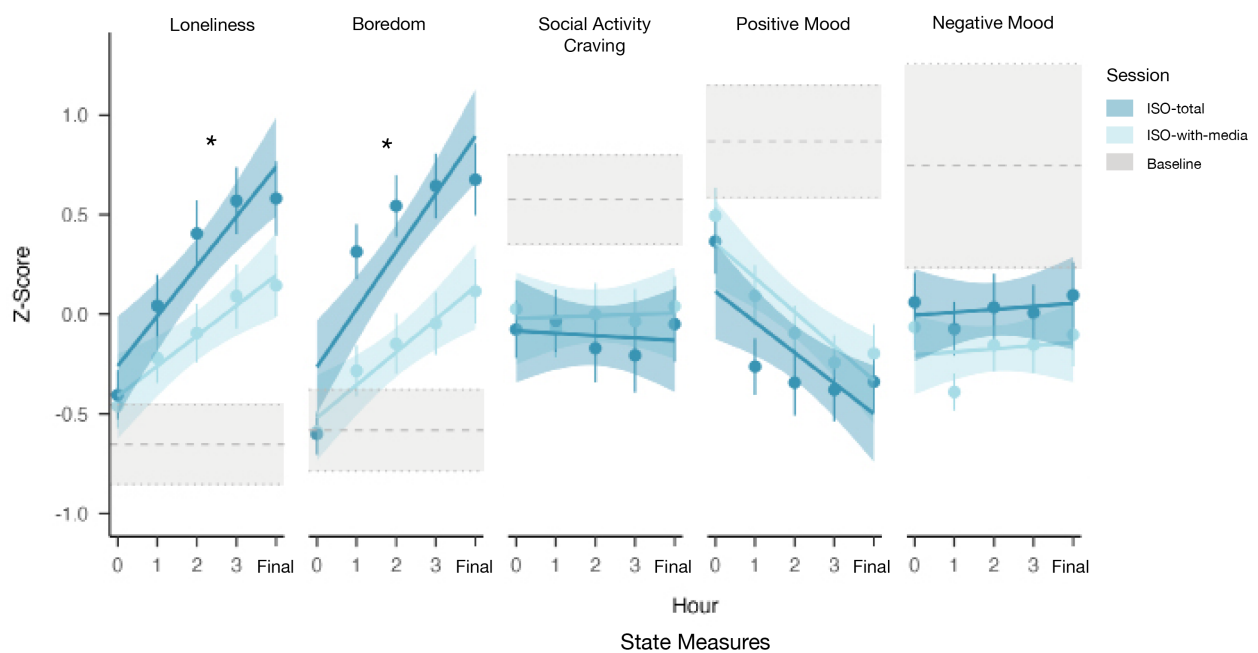
6.31, $p = .016$). Post-hoc comparisons showed that loneliness increased across the duration of isolation for both the iso-with-media ($b_{iso-with-media} = 4.03, SE = 0.76, t(5.29) < .001$) and the iso-total ($b_{iso-total} = 6.65, SE = 1.0, t(38.9) = 6.69, p < .001$) sessions (i.e., showed hourly increases). Further, the increase was steeper in the iso-total compared to the iso-with-media session ($b_{iso-total > iso-with-media} = 2.62, SE = 1.04, t(38.9) = 2.51, p = .016$). For boredom there was a two-way interaction between hour and session ($F(1, 54.58) = 7.64, p = .008$). Post-hoc comparisons showed that boredom increased across the duration of isolation for both the iso-with-media ($b_{iso-with-media} = 4.71, SE = 0.96, t(39) < .001$) and the iso-total ($b_{iso-total} = 8.31, SE = 0.96, t(39) = 4.93, p < .001$) sessions (i.e., showed hourly increases). Further, the increase was steeper in the iso-total compared to the iso-with-media session ($b_{iso-total > iso-with-media} = 3.6, SE = 1.3, t(39) = 2.76, p = .009$). Positive mood showed a significant main effect of hour ($F(1, 39.32) = 42.28, p < .001$) declining across the isolation period ($b = -1.32, SE = 0.25, t(40.94) = -5.24, p < .001$). There was also a main effect of session, which showed that positive mood was slightly higher overall in the iso-with-media session compared to the iso-total session when considering all time points ($b_{iso-with-media} = 1.87, SE = 0.25, t(40.94) = -5.24, p = .021$). However, the session by hour interaction was not significant. Social activity craving and negative mood showed no main effects or interactions in this set of analyses.

2.3.2 Threat Learning

For **arousal** ratings, there was a two-way interaction between session and cue ($F(2, 877) = 8.63, p < .001$) and between cue and phase ($F(3, 877) = 17.19, p < .001$) (Figure 2.5). Post-hoc comparisons (contrasts of threat responding) showed increased arousal ratings (higher anxiousness) to the threat cue after *acquisition* in both isolation sessions compared to baseline. Further, arousal ratings to the threat cue after *extinction* remained elevated after iso-total compared to baseline. Post-hoc comparisons (contrasts of threat discrimination) showed a greater difference between the threat cue and safety cue after *acquisition* in both isolation sessions compared to baseline. For full results, see the supplement.

For **valence** ratings, there was a two-way interaction between session and cue ($F(2, 813) = 12.68, p < .001$) and between cue and phase ($F(3, 813) = 7.11, p < .001$) (Figure 2.6). Post-hoc comparisons (contrasts of threat responding) showed increased valence ratings (higher unpleasantness) to the threat cue after *acquisition* in both isolation sessions compared to baseline. Valence ratings to the threat cue after *extinction* also remained elevated after iso-total compared to baseline. Further, valence ratings to the threat cue at *retention* remained elevated after iso-total compared to baseline. Post-hoc comparisons (contrasts of threat discrimination) showed a greater difference between the threat cue and safety cue after *acquisition* in both

Figure 2.4 Psychological State - Hourly

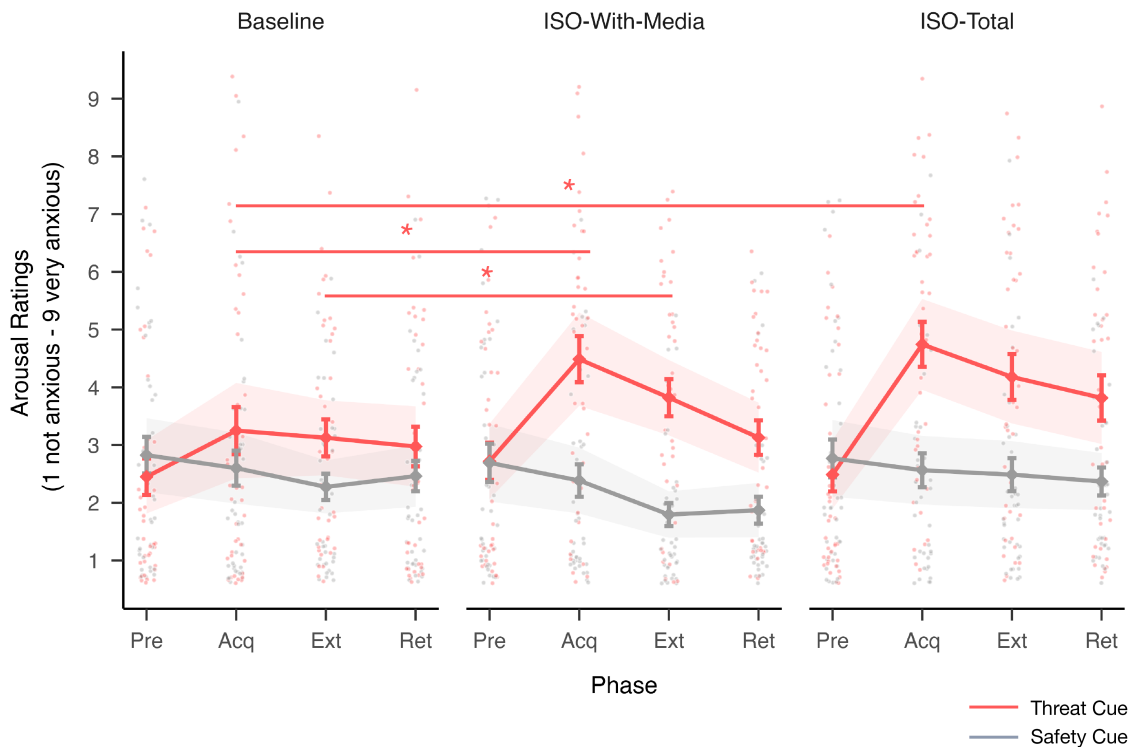


Note. The hourly effects of isolation on participants' psychological state (state loneliness, boredom, social activity craving, positive and negative mood). Points indicate estimated marginal means for each psychological state variable per hour, and bars indicate standard errors around the estimated marginal means. Lines indicate estimated linear trends and their 95% confidence intervals. Stars represent a significant hour by session interaction in post-hoc pairwise comparisons of estimated marginal trends (Bonferroni corrected for multiple comparisons [adjusted $\alpha = .025$]), indicating a difference in the linear trend between the iso-with-media and iso-total session. Psychological state variables were measured only once at baseline and those measurements are shown for reference purposes in grey (estimated marginal means are indicated by the middle dotted grey line and grey ribbons indicate the standard errors around the estimated marginal means).

isolation sessions compared to baseline. There was also a greater difference between the threat cue and safety cue at *retention* after iso-total compared to baseline. For full results, see the supplement.

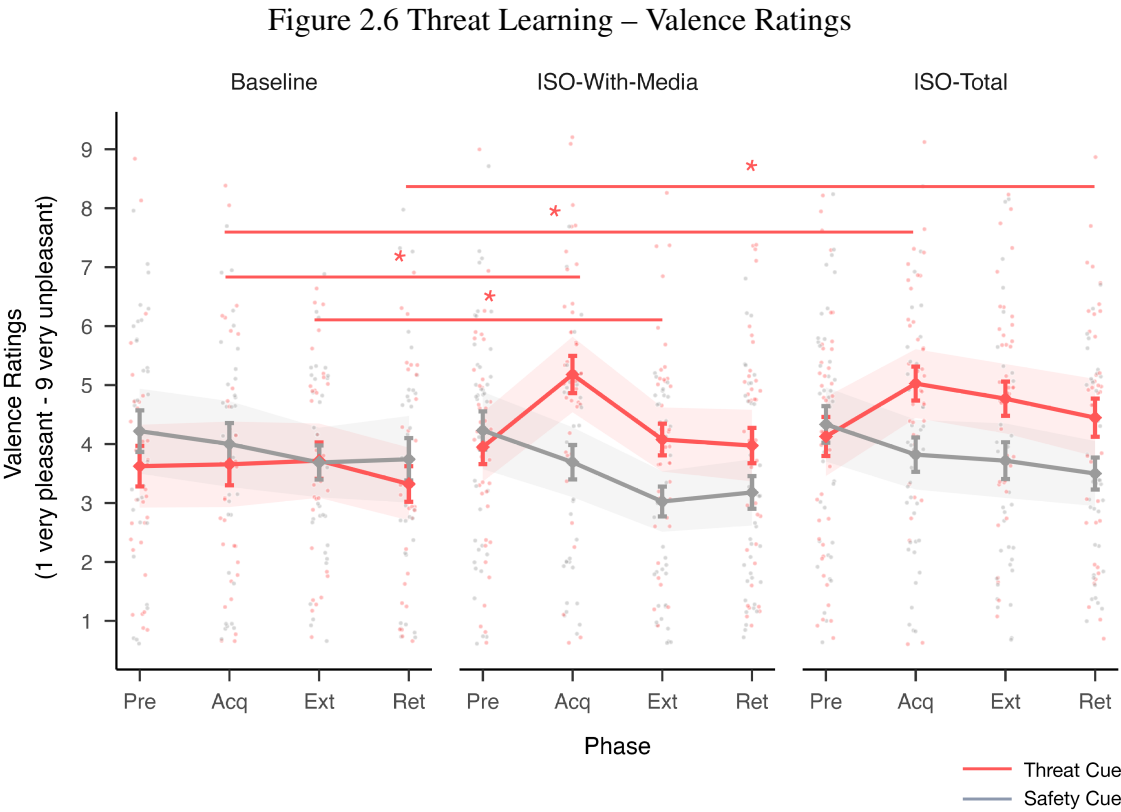
For **electrodermal activity**, there was a two-way interaction between session and phase ($F(4, 645) = 4.38, p = .002$) (Figure 2.7). Post-hoc comparisons (contrasts of threat responding) showed increased electrodermal activity to the threat cue during *extinction* in the iso-with-media session compared to baseline. Further, electrodermal activity to the safety cue during *extinction* was also elevated in both isolation sessions compared to baseline. For full results, see the supplement.

Figure 2.5 Threat Learning – Arousal Ratings



Note. This figure illustrates arousal ratings for the threat and safety cue across sessions (baseline, iso-with-media, and iso-total) and phases (Pre = pre-acquisition, Acq = acquisition, Ext = extinction, and Ret = retention). Points indicate individual participant responses, diamonds indicate the estimated marginal means, bars indicate standard errors of the estimated marginal means, and ribbons indicate the 95% confidence intervals around the estimated marginal means. Lines (with stars) indicate a significant difference in post-hoc pairwise comparisons (contrasting session effects for each cue at each phase)(Bonferroni corrected for multiple comparisons [adjusted alpha = .005])(See the supplement for the full list of post-hoc comparisons). *Source: Reproduced from Towner, E., Thomas, K., Tomova, L., & Blakemore, S.-J. (2024). Royal Society Open Science. CC-BY 4.0.*

Prior to beginning the threat learning task (pre-acquisition), there were no differences in arousal ratings or valence ratings to the threat or safety cue (or in the difference between the threat and safety cue) between any of the sessions (there was no pre-acquisition phase for electrodermal activity). The two isolation sessions (iso-with-media and iso-total) did not significantly differ from each other in threat responding or threat discrimination for any of the reported results above. There were no significant differences in ratings (arousal ratings nor valence ratings) or electrodermal activity to the aversive sound alone [unconditioned stimulus] between the three sessions (see the supplement). Further, sensitivity analyses provided



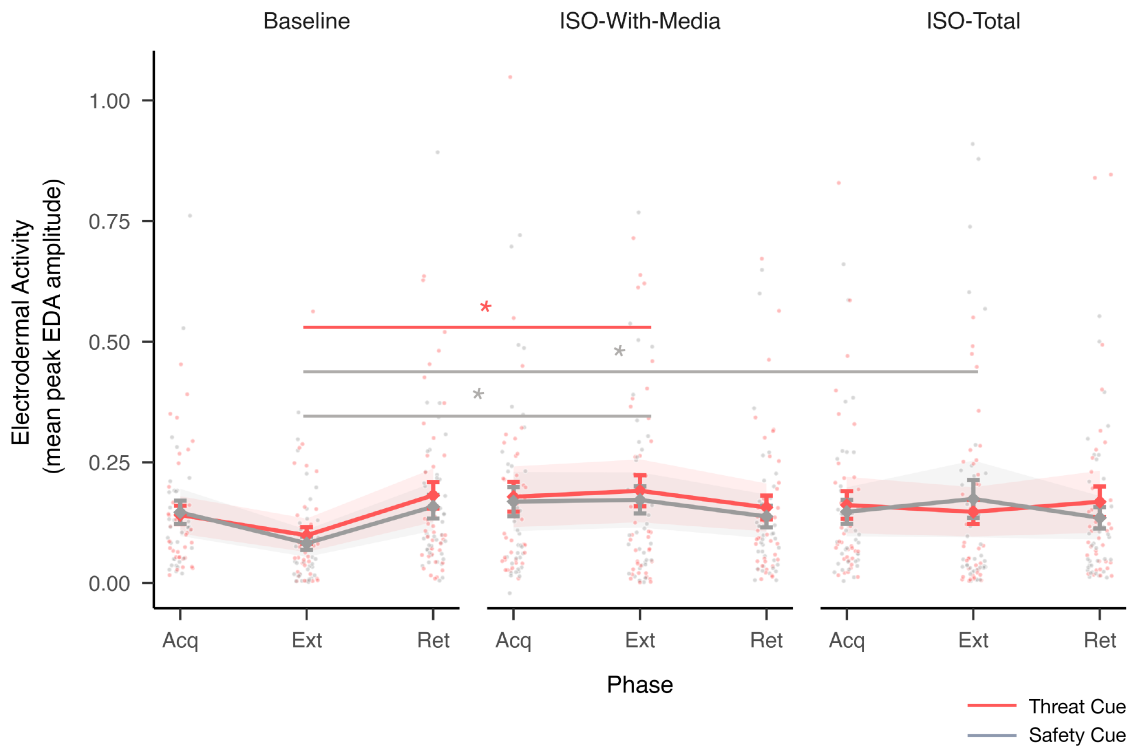
Note. This figure illustrates valence ratings for the threat and safety cue across sessions (baseline, iso-with-media, and iso-total) and phases (Pre = pre-acquisition, Acq = acquisition, Ext = extinction, and Ret = retention). Points indicate individual participant responses, diamonds indicate the estimated marginal means, bars indicate standard errors of the estimated marginal means, and ribbons indicate the 95% confidence intervals around the estimated marginal means. Lines (with stars) indicate a significant difference in post-hoc pairwise comparisons (contrasting session effects for each cue at each phase)(Bonferroni corrected for multiple comparisons [adjusted alpha = .005])(See the supplement for the full list of post-hoc comparisons). *Source: Reproduced from Towner, E., Thomas, K., Tomova, L., & Blakemore, S.-J. (2024). Royal Society Open Science. CC-BY 4.0.*

no evidence that order effects contributed to any of the results (for further details see the supplement).

2.3.3 Mechanisms

The path-analytic framework (see methods for details) demonstrated that isolation influenced threat learning *through* state loneliness and boredom (Figure 2.8), but not through other measured state variables (social activity craving, positive mood, negative mood, or state anxiety). Notably, isolation influenced threat learning through state loneliness and boredom in opposite ways. *Increased* state loneliness in the iso-total condition (compared to the iso-with-

Figure 2.7 Threat Learning – Electrodermal Activity

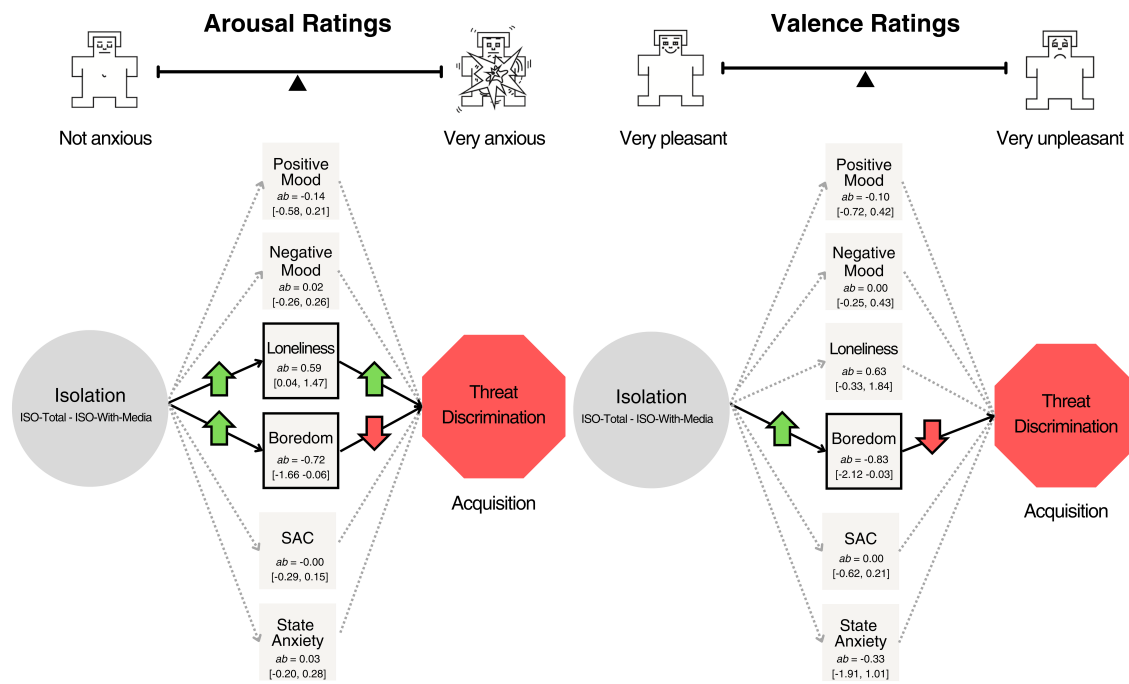


Note. This figure illustrates electrodermal activity for the threat and safety cue across sessions (baseline, iso-with-media, and iso-total) and phases (Acq = acquisition, Ext = extinction, and Ret = retention). Points indicate individual participant responses, diamonds indicate the estimated marginal means, bars indicate standard errors of the estimated marginal means, and ribbons indicate the 95% confidence intervals around the estimated marginal means. Lines (with stars) indicate a significant difference in post-hoc pairwise comparisons (contrasting session effects for each cue at each phase) (Bonferroni corrected for multiple comparisons [adjusted alpha = .005]) (See the supplement for the full list of post-hoc comparisons). *Source:* Reproduced from Towner, E., Thomas, K., Tomova, L., & Blakemore, S.-J. (2024). *Royal Society Open Science*. CC-BY 4.0.

media session) was associated with *increased* threat discrimination between the iso-total and iso-with-media sessions, as measured by arousal ratings after acquisition (while controlling for all other state variables) ($ab = 0.59$, 95% bootstrap CI = [0.04, 1.47]). In contrast, *increased* boredom in the iso-total compared to iso-with-media session was associated with *decreased* threat discrimination between the iso-total and iso-with-media sessions, as measured by arousal after acquisition (while controlling for all other state variables) ($ab = -0.72$, 95% bootstrap CI = [-1.66, -0.06]). *Increased* boredom in the iso-total (compared to iso-with-media session) was also associated with *decreased* threat discrimination between the iso-total and iso-with-media sessions, as measured by valence ratings after acquisition (while controlling for all other

state variables)($ab = -0.83$, 95% bootstrap CI = $[-2.12, -0.03]$). The full set of results are reported in the supplement.

Figure 2.8 Mechanisms



Note. This figure reports the results of the parallel multiple mediation (i.e., to what extent did increased isolation [iso-total – iso-with-media] influence threat learning [threat discrimination] *through* each state variable, while controlling for all other state variables) after *acquisition*. The left figure is for arousal ratings. The right figure is for valence ratings. Estimates (ab) are of the indirect effects. 95% confidence intervals around the indirect effects are reported in brackets. We interpreted confidence intervals that did not overlap with zero as meaningful (solid arrows and squares with black outlines)(arrows indicate direction of the effect). *Source:* Reproduced from Towner, E., Thomas, K., Tomova, L., & Blakemore, S.-J. (2024). *Royal Society Open Science*. CC-BY 4.0.

2.4 Discussion

In this experimental study, the effects of social isolation, both with and without access to digital social interactions, on psychological state and threat learning in human adolescents (aged 16 – 19) were investigated. Participants were tested at baseline and after they underwent two sessions of experimental isolation: one of total social isolation and another of social isolation with access to digital social interactions (counterbalanced). Self-reported psychological state (loneliness, boredom, social activity craving, mood and anxiety) and threat learning using a

classical Pavlovian threat conditioning task were measured, assessing both explicit (self-report ratings) and implicit (electrodermal activity) threat responses.

Self-reported state *loneliness* increased across the duration of experimental isolation in this study and was higher after total isolation compared to isolation with access to digital social interactions. Participants reported feeling lonelier at the end of the total isolation period than they did at the beginning and, interestingly, this was also true when adolescents had access to digital social interactions during isolation. However, the increase in self-reported state loneliness was higher following total isolation compared to isolation with digital social interactions. Further, *threat learning* was heightened after social isolation, irrespective of access to digital interactions. Adolescents demonstrated marked increases in explicit threat discrimination (i.e., the difference between the threat and safety cue) after both isolation sessions compared to baseline, as evidenced by self-report responses. This increased threat discrimination was evident after the acquisition phase and remained partially elevated during the extinction and retention phases. Implicit responses, as measured by electrodermal activity, showed some evidence of elevation during extinction in both isolation sessions compared to baseline. Although digital social interactions alleviated self-reported state loneliness, they did not result in significant differences in threat learning between the two isolation sessions (iso-with-media and iso-total). This suggests that while digital social interactions partially remediated the effects of isolation on feelings of loneliness they did not remediate the effects on threat learning.

Though isolation effects on electrodermal activity during *acquisition* were not observed, prior studies investigating threat learning have shown that discrepancies often arise between explicit responses (self-reported ratings) and implicit responses (electrodermal activity; Manassero et al., 2019; Oyarzún et al., 2019). Further, past research suggests that threat learning involves two separate brain circuits (Hamm and Vaitl, 1996; LeDoux, 1993). The first an "implicit" affective learning system (LeDoux, 1993) and the second an "explicit" cognitive learning system, tied to the acquisition of knowledge about threats and the conscious experience of fear (LeDoux and Brown, 2017; Purkis and Lipp, 2001). Relatedly, electrodermal activity was partially elevated to both the threat and the safety cue during *extinction*, in contrast to self-report responses. The inverse of threat learning (i.e., learning that a cue predicts an aversive stimulus) is safety learning. In the task used in this study, this translated to learning that one of the cues predicted the absence of the aversive stimulus. Threat and safety learning are related but distinct phenomena. Researchers have posited that learning about safety is more cognitively demanding than learning about threat (Grasser and Jovanovic, 2021), that safety learning might be differentially affected by exposure to stress, and that the effect of increased threat responses to safety cues are robust across anxiety disorders (Duits et al., 2015; Lissek

et al., 2005). Age-related differences in threat generalisation (i.e., the broadening of the threat response beyond the original threat stimulus) have also been found, with adolescents reporting less discrimination between threat and safety cues than adults (Lau et al., 2011). In this study, whereas self-report responses indicated increased explicit threat discrimination after acquisition, the finding that electrodermal activity was elevated to both threat and safety cues might suggest generalisation of implicit, physiological threat responses during extinction.

The parallel mediation analysis demonstrated that state loneliness exerted a significant influence on explicit threat learning in the experiment. Participants who felt a heightened sense of loneliness during the study learned to discriminate between threat and safety cues more robustly. When accounting for other state variables as parallel mediators, an indirect positive effect of isolation on explicit threat learning through state loneliness was isolated. Further, boredom played a contrasting role. To the extent participants felt lonelier in the iso-total compared to iso-with-media session, they showed increased threat learning (controlling for all other state variables). To the extent participants felt more bored in the iso-total compared to iso-with-media session, they showed decreased threat learning (controlling for all other state variables). Thus, state loneliness and boredom had opposing effects. Substantial measures were taken to minimise boredom in the isolation sessions; however, boredom was indeed still higher in both isolation sessions than in baseline, and higher in the iso-total than in the iso-with-media session. This might explain the lack of differences in threat learning between the two isolation sessions: heightened boredom in the iso-total compared to iso-with-media session might have counteracted the effects of heightened state loneliness (perhaps by decreasing overall levels of arousal or by reducing attention and engagement with the threat learning task)(see Danckert and Elpidorou, 2023 for a review discussing the functional purpose of boredom). Considering that participants were confined to predetermined activities in a controlled experimental setting in this study, in real-world situations where state loneliness and boredom are not as highly correlated, for example, where people are allowed to choose their own activities, the impact of isolation on threat learning might be stronger than observed here. However, loneliness and boredom could be interconnected constructs, which are difficult to disentangle entirely. For many people, it appears to be fundamentally boring to be on one's own. We speculate that boredom might be a feature of loneliness.

Overall, the current study replicates findings observed in animal (rodent) models, where increased threat conditioning and diminished threat extinction have been observed following social isolation (Lukkes et al., 2009a; Matsuda et al., 2018; Skelly et al., 2015). The results replicate these findings in human adolescents. Furthermore, these data bridge the gap between animal research and previous human studies, which have indicated that individuals with pre-existing chronic loneliness tend to exhibit higher rates of fear relapse in threat learning

paradigms similar to the one used in this study (Hornstein and Eisenberger, 2022). Notably, in this study, even a short period of experimentally induced social isolation led participants to display enhanced threat learning compared to at baseline. This helps clarify potential ambiguities regarding the direction of causality in prior nonexperimental human research (i.e., those that found correlations between chronic loneliness and threat learning), positioning social isolation as a plausible causal contributor to heightened threat vigilance.

Chapter 3

The Effects of Social Isolation on Adolescent Reward Responsiveness

A version of this chapter has been published:

Tomova, L., Towner, E., Thomas, K., Zhang, L., Palminteri, S., & Blakemore, S.-J. (2025). Acute isolation is associated with increased reward seeking and reward learning in human adolescents. *Communications Psychology*, 3(1), 135. DOI: 10.1038/s44271-025-00306-6

3.1 Introduction

The previous chapter investigated the effects of acute social isolation on threat learning in human adolescents. Reward processing is another domain of particular importance due to its impact on behaviour and well-established associations with mental health outcomes (Berridge and Robinson, 2003). For example, research on reward processing and its underlying neurobiology has offered valuable insights into various psychological disorders, including substance abuse, eating disorders, obsessive behaviours and depression (Berridge and Robinson, 2003). Consistent with findings in adults, adolescent depressive symptoms have been associated with neural deficits in both anticipatory and consummatory reward processing compared to healthy adolescents (Thompson et al., 2023). Additionally, a longitudinal study tracking individuals from childhood to adolescence demonstrated a bidirectional association between stress and reward processing (Vidal-Ribas et al., 2019). The results suggest that stress might impair reward anticipation, while reduced reward anticipation might simultaneously increase vulnerability to stress. In typically developing adolescents, reward processing undergoes marked changes (discussed in Section 1.2). Research demonstrates that healthy adolescents

exhibit heightened behavioural and neural sensitivity to rewards, particularly social rewards. Alterations in reward processing have also been thought to underlie adolescent differences in risk-taking. Researchers have posited that the increase in risky behaviours observed in adolescents when amongst peers might stem from the heightened reward value of social interactions during this period of life, potentially motivating adolescents to engage in riskier behaviours to gain peer approval (Foulkes and Blakemore, 2016). As mentioned in Section 1.7, neural reactivity in brain regions associated with motivation and reward processing were found to be altered by social media use across adolescence in a longitudinal study (Maza et al., 2023). Another study that used a computational approach to model real-world social media data found that adolescents' social media engagement was more strongly motivated by their response to social reward (likes) compared to adults (Da Silva Pinho et al., 2024). Importantly, however, differences in adolescent reward processing might serve adaptive developmental functions. A recent review highlighted the idea that the strong engagement of reward circuitry is important for motivating learning, exploration and beneficial social behaviours in adolescents (Silvers and Peris, 2023). Moreover, optimal levels of reward sensitivity might be best for healthy adolescent development given that reduced reward sensitivity has been linked to an increased risk for depression (Forbes, 2020; Keren et al., 2018; McCabe, 2018) and heightened reward sensitivity might confer vulnerability to risk-taking behaviours and substance use (de Water et al., 2017; Galvan et al., 2007; Rao et al., 2011).

Given that adolescence involves significant reward-related developmental changes, adolescents might be particularly susceptible to the effects of social isolation on reward processing. Experimental studies in animal models have consistently shown that isolating adolescent animals primarily affects dopaminergic brain reward circuits and alters reward seeking and reward learning (Hall, 1998; Novick et al., 2018). As mentioned in Section 1.3.3 social isolation in adolescence has been shown to increase sensitivity to social rewards Ikemoto and Panksepp (1992) and also increase seeking of food and drug rewards in rodents (McCool and Chappell, 2009). Conversely, operant access to social interaction has been shown to prevent drug self-administration in rats (Venniro et al., 2018). Research has further shown that social isolation also changes reward *learning* in adolescent animals. Specifically, studies have found that adolescent rats exposed to social isolation exhibited increased initial reward learning (Hall, 1998; Novick et al., 2018), but required more sessions to reverse probabilistically learned rewards, and were slower to adjust their task strategy when reward contingencies changed, compared to socially housed rats (Amitai et al., 2014; Jones et al., 1991). This suggests that social isolation might diminish cognitive flexibility. Separately, socially isolated adolescent rats have demonstrated stronger reward learning to social versus amphetamine paired contexts, whereas isolated adult rats showed the opposite pattern (Yates et al., 2013). That adolescent

rats learned from social rewards more than from drug rewards when deprived of social contact suggests that social contact acts as a powerful reward signal in adolescence. Indeed, one study found synergistic effects of social and drug rewards, where social reward enhanced the rewarding effects of drugs in adolescent rats (Reyna et al., 2021).

In human adolescents, evidence regarding the relative significance of social versus nonsocial rewards remains inconclusive, largely because few studies have directly compared these reward types within the same paradigm. As discussed in Section 1.2, some studies have demonstrated heightened adolescent sensitivity to social compared to nonsocial rewards (Andrews et al., 2019; Ethridge and Weinberg, 2018). Conversely, other studies have shown increased adolescent sensitivity to monetary versus social rewards (Hwang et al., 2017; Kohls et al., 2009; Wang et al., 2020). However, the relationship between social and nonsocial reward sensitivity in adolescents might be more nuanced, with evidence suggesting context-dependent variations. For instance, blunted neural responses to social rewards (but not monetary rewards) predicted increased depressive symptoms in late adolescents during the COVID-19 pandemic (Freeman et al., 2023). Similarly, the interaction between social reward responsiveness and rejection sensitivity predicted depressive symptoms in late adolescents, where individuals with high rejection sensitivity combined with low social reward responsiveness exhibited greater depressive symptoms (Pegg et al., 2021). Furthermore, a recent systematic review found that adolescents who experienced early life interpersonal stress demonstrated reduced social reward sensitivity, manifesting as lower accuracy and higher thresholds for identifying happy faces (Bick et al., 2017; Diaconu et al., 2023; Koizumi and Takagishi, 2014; Palacios-Barrios et al., 2023). These findings suggest that differences in social versus nonsocial reward processing in adolescents might depend on social context – such as, for example, social isolation.

While results from animal studies show strong evidence for the effects of social isolation on reward processing, it is unclear to what extent these findings can be translated to human adolescents. Unlike the animal literature, in humans there is a lack of experimental studies which directly manipulate social isolation and investigate its effects on reward responsiveness, though non-experimental studies have provided some insights. During the COVID-19 pandemic, one study found a link between objective daily social interactions and motivational behaviour in older adolescents (Gigli et al., 2024). Findings showed that greater social isolation (less time spent with others) correlated with an increased sensitivity to rewarding stimuli and a decreased impact of a reward on subsequent choice behaviour. Separately, another study of older adolescents found that feelings of social disconnection drove social reward-seeking behaviour on social media (disconnection motivated greater use; Sheldon et al., 2011). Further, a few studies in adults have shown associations between loneliness and reward-related neural circuitry (Cacioppo et al., 2009; Canli et al., 2017; Inagaki et al., 2016). Indeed, a recent

review suggested that altered reward processing might be one mechanism by which loneliness influences depression (Wilkialis et al., 2021). However, as mentioned in Chapter 2, these correlational studies do not enable causal inferences. Experimental studies in humans can investigate the effects of social isolation on reward responsiveness and whether there are different effects when participants are physically isolated but have access to digital social interactions.

3.1.1 Aims

In this chapter, the effect of acute isolation, with and without digital social interactions, on reward responsiveness in human adolescents aged 16 – 19 years is investigated. As described in Chapter 2, participants underwent three sessions in this study, starting with baseline and followed by two isolation sessions of up to four hours. One isolation session (iso-total) involved isolation from all social interactions, while the other (iso-with-media) allowed for digital social interactions only. At each session (baseline, iso-total and iso-with-media), reward seeking and reward learning were measured using an effort-based decision making task and a reinforcement learning task, respectively. Here, I focus on three research questions: (Q1) How does acute isolation impact reward responsiveness (including reward seeking and reward learning)?; (Q2) Do digital social interactions alter the effects of acute isolation on reward responsiveness?; and (Q3) Do these effects differ depending on whether rewards are social or non-social? It was hypothesised that isolation would increase reward seeking and initial reward learning, but diminish reversal learning, and that these effects would be stronger for social versus non-social rewards. It was also hypothesised that digital social interactions might lessen the effects of isolation on reward seeking and reward learning.

3.2 Methods

This chapter is a part of the social isolation study described in the previous chapter (Chapter 2). Therefore the participants, procedures and study design in this chapter are identical to those described in the previous chapter.

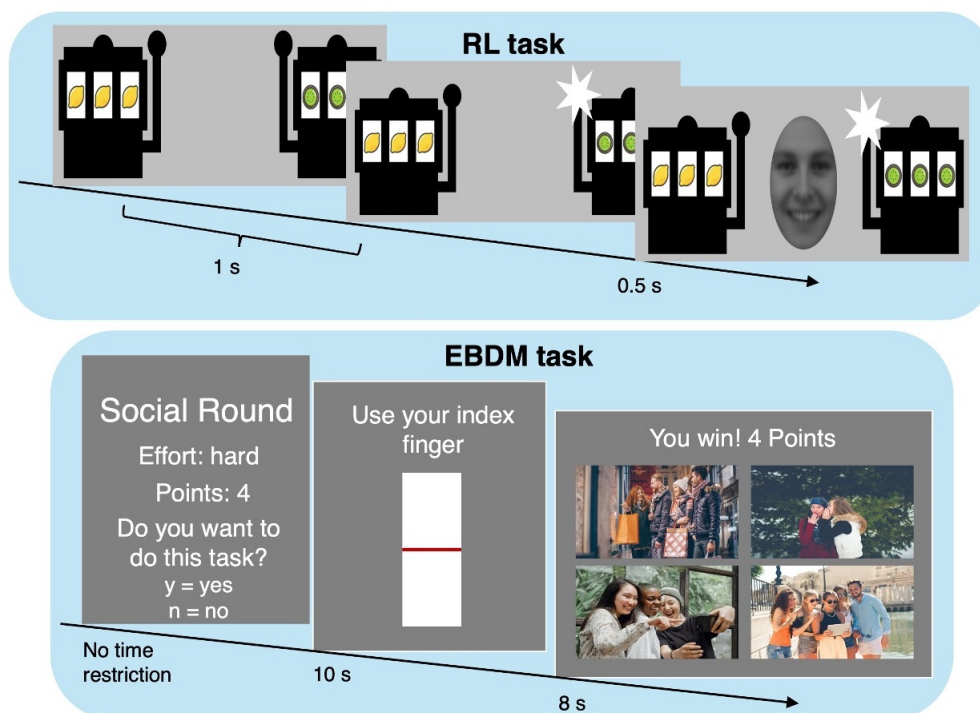
3.2.1 Measures

3.2.1.1 Questionnaires

The questionnaires collected at the start of testing in each of the three sessions (baseline, iso-with-media, iso-total) measuring participants psychological state (state loneliness, social activity

craving, boredom, mood, state and trait anxiety and depression) as well as the questionnaire asking about digital social interactions during the isolation period (iso-with-media session), were identical to those described in the previous chapter. Reward responsiveness was measured using the tasks described below (Figure 3.1).

Figure 3.1 Reward Responsiveness Tasks



Note. Timelines of example trials for each reward task. *Bottom*) Effort-based decision making (EBDM) task. On each trial, participants were first shown a screen that listed details for the upcoming trial. These included level of effort (hard, easy), reward (high [4 points], low [1 point]) and context (social, nature). Participants were asked whether they wanted to complete that trial. Response time (RT) was measured while participants decided if they wanted to complete the trial. If they chose yes, they saw a bar that they were required to pump up in 10 s (the amount of effort required was calibrated to each participant's maximum effort levels assessed at the start of the task in each session) and, if they were successful, they saw a screen indicating how much they had won (1 or 4 points) images depicting social interactions or nature landscapes, depending on context (low reward = 1 image; high reward = 4 images). *Top*) Reinforcement learning (RL) task. Participants were presented with two slot machines and asked to choose one. After they chose, they received feedback as to whether they had won (indicated by a smiling face or a plus symbol) or did not win (indicated by a neutral face or a zero). *Source:* Reproduced from Tomova, L., Towner, E., Thomas, K., Zhang, L., Palminteri, S., & Blakemore, S.-J. (2025). *Communications Psychology*. CC-BY 4.0.

3.2.1.2 Effort-Based Decision Making Task

During testing in each of the three sessions (baseline, iso-with-media and iso-total) **reward seeking** was measured using an effort-based decision making (EBDM) task (an adapted version of the Effort Expenditure for Rewards Task (EEfRT; Treadway et al. 2009). In the adapted version, reward and effort were manipulated and orthogonalised. Participants were presented with a series of trials with different combinations of high rewards and low rewards for successfully completing "hard tasks" and "easy tasks". First, participants underwent two calibration trials in which the task measured their maximum effort (the maximum number of button presses performed in 10 s using their index finger). Based on this, "hard task" trials required participants to make 80% of the maximal button presses they managed in 10 s to succeed. "Easy task" trials required participants to make 40% of the maximal button presses they managed in 10 s to succeed. Rewards earned could be either 1 point (low reward) or 4 points (high reward).

In addition, the study aimed to determine whether the effects of isolation on reward seeking were specific to social (versus nonsocial) rewards. To investigate this specificity, an element of context (social versus nonsocial) was added to the effort-based decision making task. A previous study showed that adolescents enjoy looking at pictures depicting social content more than looking at nonsocial pictures of landscapes (Andrews et al., 2019) and that this affected their choice behaviour. Therefore, in addition to earning points, participants could also see pictures corresponding with each trial's context and reward magnitude. For the high-reward trials in the social context, participants could see four social pictures (e.g. pleasant pictures of people hugging, laughing together, etc.). For the high-reward trials in the nonsocial context, participants could see four nature pictures (e.g. pleasant pictures of mountains, beaches, rivers, etc.). For the low-reward trials, participants could see one picture corresponding to the trial's context. Picture stimuli were taken from Andrews et al. (2019).

Before each trial, participants were presented with the combination of the upcoming context (social versus nonsocial), required effort (hard versus easy) and potential reward (high versus low) before deciding whether they wanted to perform each trial's task (there was no time restriction on this decision). If participants completed the trial successfully (i.e., pumped up the bar within the time limit), they were shown the points they won as well as the corresponding photo(s) for 8 s. After each trial, a fixation cross was presented for 0.5 s. In this task, combining the three two level factors (effort, reward and context) created eight conditions. There were six trials per condition (48 trials in total), presented in random order. Points attained during the task were converted into monetary winnings at the end of each session¹.

¹Each point equalled two pence and participants received the cumulative earnings they made across the whole task (which was up to £2.50). Participants were told that each point they won on the task would translate to actual

3.2.1.3 Reinforcement Learning Task

During testing in each of the three sessions (baseline, iso-with-media and iso-total) **reward learning**, or the ability to learn stimulus–reinforcement associations and to reverse them based on probabilistic feedback, was measured using a probabilistic reinforcement and reversal learning task (Ahn et al., 2017; Metha et al., 2019). In this task, participants were shown two slot machines and asked to choose between them to obtain a reward. One slot machine was rewarded 80% of the time; the other was rewarded 20% of the time. Participants needed to learn from feedback (through trial and error) which slot machine was rewarded more often. After 7 trials, the reward contingencies switched and participants needed to learn the new reward contingencies. Feedback was given via symbols (nonsocial feedback) and facial expressions (social feedback) in counterbalance blocks. Social and nonsocial feedback were included to determine whether the effects of isolation on reward learning were specific to feedback type. Rewards (positive feedback) were represented by either a plus symbol (+; non-social) or a smiling face (social), while the absence of a reward (negative feedback) was represented by a zero symbol (0; non-social) or a neutral face (social). The task was comprised of two blocks with 28 trials per block (in total 56 trials). Reversals created four distinct phases of the task (phase 1 = acquisition, phase 2 = first reversal [reward contingencies flipped], phase 3 = second reversal [reward contingencies same as in acquisition], and phase 4 = third reversal [reward contingencies flipped again])².

The two facial pictures (smiling and neutral) were generated by averaging facial pictures of Caucasian young adults. To do this, happy and neutral faces from the Averaged Karolinska Directed Emotional Faces set (Lundqvist et al., 2015) were used. The female and male faces for each emotion (happy and neutral) were averaged, rendering them ambiguous as to sex/gender. Photoshop was used to create the averages. The images were cropped to remove the background and hair, displaying only the face. Facial pictures were displayed in black and white to match the non-social feedback. Participants were given 1 s to respond on each trial and then received feedback for 0.5 s. A fixation cross was presented for 0.5 s between each trial.

money (in addition to their participant reimbursement). Participants were not informed about the exact conversion rate but were told that the combined additional wins for both reward tasks in each session could be up to £5. There was no endowment with money in advance as the tasks did not involve any losses

²Participants were not informed about the structure of the learning task (i.e., that there would be reversals) or the probabilities of reward. Participants were only told that their task was to determine, by trial and error, which slot machine was more advantageous in order to win as many points as possible.

There were three pairs of stimuli used — the "fruits" within the slot machines³. Stimuli pairs were fully counterbalanced between participants and sessions, with participants seeing a different pair of shape stimuli in each session (to avoid carryover effects). Further, other components of the task were also randomised at each session (which side each fruit in the pair was displayed on, whether or not the first "correct" response was on the left or the right side, and whether the social or nonsocial feedback came first). Practice trials had separate stimuli that were not used in the rest of the task.

3.2.2 Data Analysis

3.2.2.1 Reward Seeking

Reaction times (RTs) in choosing to undergo an effortful task have been shown to be indicative of strength of preference (Konovalov and Krajbich, 2019). Therefore, mixed effects models were used to investigate the fixed effects of session, context, reward and effort on choice RTs (log-transformed; Gelman and Hill, 2006) for trials in which participants decided to complete the effortful task. Participant was included as a random effect (allowing intercepts and slopes to vary between participants; Barr et al. 2013) and iso-total served as the reference session. Calibration (i.e., the number of button presses participants managed at the beginning of each session from which hard and easy tasks were calculated) was added as a control variable. The formula for this model is displayed in Equation 3.1.

$$\begin{aligned} \text{ChoiceRT} = & \text{session} \times \text{effort} \times \text{reward} \times \text{context} + \text{calibration} + \\ & (\text{session} \times \text{effort} \times \text{reward} \times \text{context} | \text{participant}) \end{aligned} \quad (3.1)$$

3.2.2.2 Reward Learning

To investigate reward learning, measures of behavioural performance as well as computational parameters of learning were calculated.

Performance. Performance in each phase of the task was quantified in three ways: choice RTs⁴, accuracy and perseverative errors. Choice RTs on each trial were quantified in seconds

³Stimulus pairs were the following: Pair 1 = Cherries and Grapes; Pair 2 = Watermelon and Banana; Pair 3 = Lemon and Kiwi. Participants were assigned an order (A,B,C). If their order was A, they saw Pair 1 in their first session (baseline), Pair 2 in their second session, and Pair 3 in their third session. If their order was B, they saw Pair 2 in their first session (baseline), Pair 3 in their second session, and Pair 1 in their third session. If their order was C, they saw Pair 3 in their first session (baseline), Pair 1 in their second session, and Pair 2 in their third session.

⁴Because our version of the task included a time limit for responding (1 s), fast responding was advantageous.

and were log-transformed. Accuracy was quantified as the proportion of correct responses during each phase. Perseverative errors were quantified as the proportion of errors in each reversal phase.

The effects of the three categorical variables: session (baseline, iso-total, iso-with-media), feedback (social, nonsocial) and phase (acquisition, first reversal, second reversal, third reversal) on choice RTs and accuracy were tested using mixed effects models, with iso-total serving as the reference group. Participant was included as a random effect (allowing intercepts and slopes to vary between participants; Barr et al. 2013). The formula for this model is displayed in Equation 3.2.

$$\text{ChoiceRT/Accuracy} = \text{session} \times \text{feedback} \times \text{phase} + (\text{session} \times \text{feedback} \times \text{phase} | \text{participant}) \quad (3.2)$$

For perseverative errors, a similar model (Equation 3.3) was used, but each reversal phase was analysed separately. This allowed an assessment of the effects of session on updating of previously learned reward contingencies when participants experienced a reversal for the first time (first reversal), when contingencies switched back to those seen during acquisition (second reversal) and when contingencies switched again (third reversal). Results were corrected using the Bonferroni method for multiple comparisons (three reversal phases – first reversal, second reversal, third reversal) for an adjusted alpha level of .016 (.05/3).

$$\text{Errors}_{\text{perseverative}} = \text{session} \times \text{feedback} + (\text{session} \times \text{feedback} | \text{participant}) \quad (3.3)$$

Computational Modelling. Using hierarchical Bayesian modelling⁵, participants' trial-by-trial choice behaviour from the reward learning task was analysed using computational reinforcement learning and decision-making models for probabilistic reversal learning tasks (Ahn et al., 2017; Metha et al., 2019)⁶. To leverage the full potential of hierarchical Bayesian analysis and capture the temporal dynamics of reinforcement learning, the models were fitted to data across all sessions, phases and feedback types simultaneously⁷. A design matrix of effect coding was constructed to reflect differences between sessions and feedback type (Figure 3.2).

⁵Computational modelling was performed using the Stan language in R via modified scripts from the hBayesDM package (Ahn et al., 2017). Using this approach, both individual and group-level parameters (i.e., posterior distributions) were estimated simultaneously in a mutually constraining fashion.

⁶For the group level means and standard deviations, normal distributions were used; see Ahn et al. (2017) for more details on model specification and parameter declaration

⁷This approach better reflected the within-participant design structure and avoided overestimating differences between conditions compared to fitting separate models for each condition.

Figure 3.2 Reward Learning Task – Design Matrix

	<i>baseline</i>	<i>iso – with – media</i>	<i>iso – total</i>	<i>baseline</i>	<i>iso – with – media</i>	<i>iso – total</i>
<i>nonsocial</i>	1	0	0	0	0	0
<i>nonsocial</i>	1	1	0	0	0	0
<i>nonsocial</i>	1	1	1	0	0	0
<i>social</i>	1	1	1	1	0	0
<i>social</i>	1	1	1	1	1	0
<i>social</i>	1	1	1	1	1	1

Note. The first three rows depict the condition with nonsocial feedback, and the last three rows depict the condition social feedback; columns were used to for sessions (coded with respect to the baseline session). For example, the second column indicates the difference between the iso-with-media and baseline session for the nonsocial feedback condition. As a result, row summaries indicate the parameters for combinations of sessions and feedback type. For example, the second row indicates the parameter in the iso-with-media condition (e.g., $X_{iso-media} = X_{baseline} + X_{iso-media-diff}$). All other rows and columns follow the same rule. This design matrix was applied to all model parameters in each candidate model under a single overall hierarchical fitting framework. *Source: Reproduced from Tomova, L., Towner, E., Thomas, K., Zhang, L., Palminteri, S., & Blakemore, S.-J. (2025). Communications Psychology. CC-BY 4.0.*

The data were fitted to four different reversal learning models⁸. Each model employs the Rescorla-Wagner value update rule (Rescorla and Wagner, 1972) but differs in terms of how information is integrated. The Rescorla-Wagner update rule assumes that individuals assign and update internal stimulus value signals based on the prediction error, i.e., the mismatch between outcome (received reward/punishment following choice of this stimulus) and prediction (expected value of choosing this stimulus). The models were as follows:

1. A reward-punishment model (den Ouden et al., 2013), which expands the classic Rescorla-Wagner model of conditioning (Rescorla and Wagner, 1972) with separate learning rates for reward and punishment trials, here treating non-wins as punishments (Equation 3.4).

$$V_{c,t} = \begin{cases} V_{c,t-1} + \eta^{rew}(O_{t-1} - V_{c,t-1}), & \text{if } O_{t-1} > 0 \\ V_{c,t-1} + \eta^{nrew}(O_{t-1} - V_{c,t-1}), & \text{if } O_{t-1} < 0 \end{cases} \quad (3.4)$$

Where, η^{rew} is the learning rate for rewards and η^{nrew} is the learning rate for non-rewards; O is the outcome received. $V_{c,t}$ is the value of choice c on trial t . $O > 0$ indicates a win and $O < 0$ indicates no win. In this model, only the chosen stimulus value is updated.

⁸Model convergence was assessed by examining R-hat values, an index of the convergence of the chains (Gelman and Rubin, 1992)

2. An experience-weighted attraction model (Camerer and Ho, 1999), which includes an "experience" weight parameter that balances between past experience and new information to increasingly tip in favour of past experience (Equations 3.5–3.6).

$$n_{c,t} = n_{c,t-1} \times \rho + 1 \quad (3.5)$$

$$V_{c,t} = (V_{c,t-1} \times \phi \times n_{c,t-1} + O_{t-1}) / n_{c,t} \quad (3.6)$$

Where, $n_{c,t}$ is the "experience weight" of the chosen stimulus on trial t , which is updated on every trial using the experience decay factor ρ . $V_{c,t}$ is the value of choice c on trial t for outcome O received in response to that choice, and ϕ is the decay factor for the previous payoffs. In this model, ϕ is equivalent to $1 - \eta$ (the inverse of the learning rate) in Rescorla-Wagner models.

3. The experience-weighted attraction model (Equation 3.5) with separate learning rates for positive and negative prediction errors. (Equation 3.7).

$$V_{c,t} = \begin{cases} (V_{c,t-1} + \phi^{rew} \times n_{c,t-1} + O_{t-1}) / n_{c,t}, & \text{if } O_{t-1} > 0 \\ (V_{c,t-1} + \phi^{nrew} \times n_{c,t-1} + O_{t-1}) / n_{c,t}, & \text{if } O_{t-1} < 0 \end{cases} \quad (3.7)$$

4. A fictitious update model (Gläscher et al., 2009), which includes an update rule for the unchosen option considering the knowledge individuals gain about the unchosen option, here with separate learning rates for positive and negative prediction errors (Equation 3.8, Equation 3.9).

$$V_{c,t} = \begin{cases} V_{c,t-1} + \eta^{rew}(O_{t-1} - V_{c,t-1}), & \text{if } O_{t-1} > 0 \\ V_{c,t-1} + \eta^{nrew}(O_{t-1} - V_{c,t-1}), & \text{if } O_{t-1} < 0 \end{cases} \quad (3.8)$$

$$V_{nc,t} = \begin{cases} V_{c,t-1} + \eta^{nrew}(-O_{t-1} - V_{c,t-1}), & \text{if } O_{t-1} > 0 \\ V_{c,t-1} + \eta^{rew}(-O_{t-1} - V_{c,t-1}), & \text{if } O_{t-1} < 0 \end{cases} \quad (3.9)$$

Where the value V of both the chosen c and unchosen nc stimulus are updated with the actual prediction error and the counterfactual prediction error per trial t , respectively. O is the outcome received. The learning rate η , which is divided into η^{rew} (learning rate for rewards) and η^{nrew} (learning rate for non-rewards) evidences the magnitude of the value update affected by both positive and negative prediction errors.

For all models, a softmax choice function was used to compute the action probability given the action values. On each trial t , the action probability of choosing option A (over B) was defined as follows (Equation 3.10).

$$p(A) = \frac{1}{1 + e^{-\beta(V_A - V_B)}} \quad (3.10)$$

Where β is the inverse temperature parameter that governs the stochasticity of the choice, computed using inverse logit transfer. Higher β values denote decisions driven by relative value whereas lower β values denote more choice stochasticity.

In the subsequent text, positive learning rates (η^{rew}) will be denoted as *learning_{pos}*, negative learning rates (η^{nrew}) will be denoted as *learning_{neg}* and inverse temperature (β) will be denoted as *beta*.

Model Comparison. Model comparison was performed to select a model that best captured the behaviour of the participants. Comparison of model fit was assessed using Bayesian bootstrap and model averaging, whereby log-likelihoods for each model were evaluated at the posterior simulations and a weight obtained for each model. Model weights were compared using four model weight metrics: leave-one-out information criterion (LOOIC), Bayesian stacking of means (Bayesian stacking), pseudo Bayesian model averaging (pseudo-BMA) and widely applicable information criterion (WAIC; Yao et al., 2018). For LOOIC and WAIC, lower values indicate better model fit. For Bayesian stacking and pseudo-BMA higher values indicate better model fit.

Hierarchical Bayesian Hypothesis Testing. Following model selection, hierarchical Bayesian hypothesis testing was used⁹ to extract and compare the group-level posterior distribution parameters (*learning_{pos}*, *learning_{neg}*, *beta*) between sessions (baseline, iso-total and iso-with-media) for each feedback type (social, nonsocial). The Savage-Dickey method was used¹⁰ (Boehm et al., 2018) which generates a Bayes factor for each pairwise comparison of interest. The Bayes factor is obtained by comparing each difference distribution to a prior distribution that expresses the expectation about the effect size of the pairwise difference $\delta = (\mu_2 - \mu_1)/\tau$, where $\mu_1, 2$ are the means of the conditions to be compared and τ is the group level standard deviation. The null hypothesis specifies that $\delta = 0$, indicating no difference between the

⁹This approach to hypothesis testing was selected because two-step approaches combining hierarchical Bayesian models with frequentist follow-up analyses have been shown to systematically underestimate variance resulting in a bias towards the alternative hypothesis (Boehm et al., 2018)

¹⁰Posterior inference was performed using Markov Chain Monte Carlo (MCMC) sampling using the mode of the posterior distribution as the summary parameter for individual participants. Four MCMC chains were used, with 1000 post-warmup iterations per chain, resulting in 4000 valid MCMC posterior samples.

conditions. The real difference distributions are then compared to this prior distribution for each case. Specifically, because the null hypothesis is $\delta = 0$, the Bayes factor is described as the prior density at $\delta = 0$ divided by the posterior density at $\delta = 0$. A Bayes factor of greater than 3 can be considered meaningful evidence in support of the alternative hypothesis (i.e., that posterior distributions of a given comparison are different from each other).

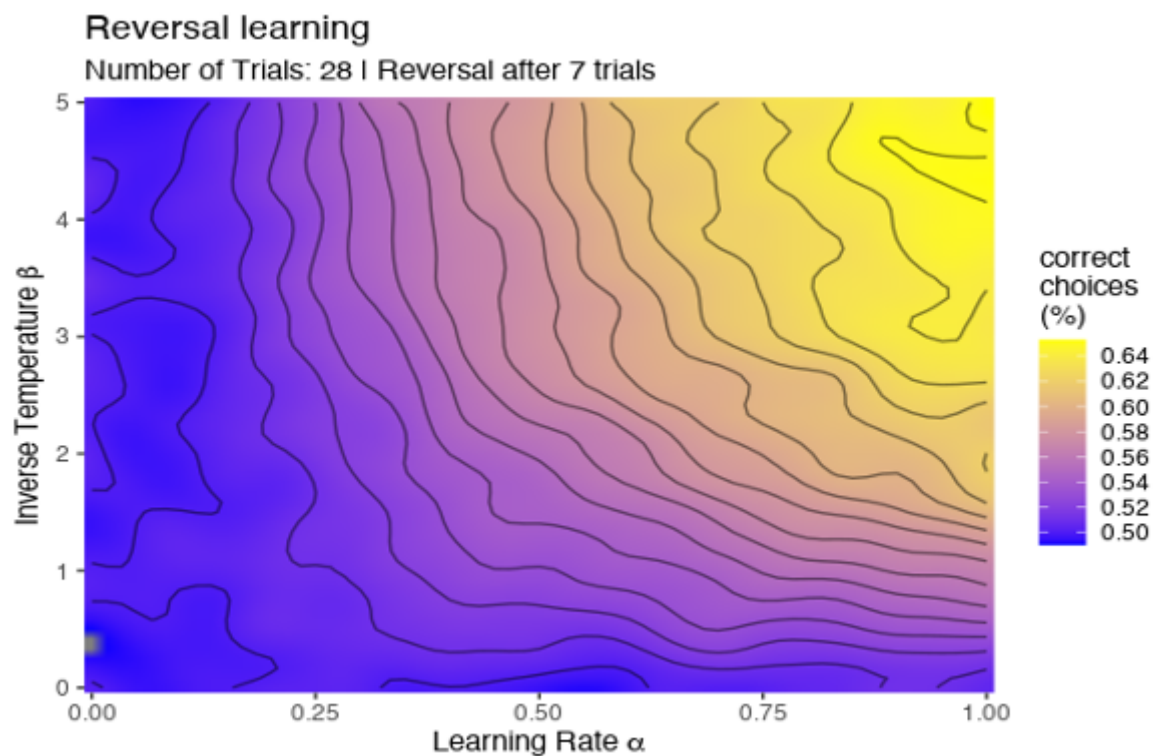
Optimal Parameter Simulations. Whether differences in parameters indicate "better" or "worse" behaviour can be heavily dependent on the task design and the values of the other relevant model parameters (Zhang et al., 2020a). Simulations were therefore used to identify the optimal learning parameters for the task environment used in this study. Optimal parameter values were considered those that resulted in the highest choice accuracy (defined as the percentage of "correct" choices, i.e., choices for options associated with a higher probability of reward). To simulate these, parameter combinations were created from a grid spanned by the learning rate (minimum value/maximum value/steps = 0/1/60) and inverse temperature (*beta*)(0/20/60). Virtual participants completed 28 trials corresponding to the number of trials in our task for each type of feedback (social, nonsocial) in each session (baseline, iso-total, iso-with-media) with a reward schedule of 80 : 20. The optimal learning rate and inverse temperature (*beta*) were defined as the average parameter values of the virtual participants with the 10 highest accuracy scores across the simulations. To reduce random noise due to the finite number of samples, the resulting images were smoothed with a Gaussian filter ($SD = 2$; Figure 3.3).

3.2.2.3 Mechanisms

As in Chapter 2, this chapter sought to explore the degree to which participants' psychological state during isolation acts as a "mechanism" by which isolation affects reward responsiveness. Here, a simplified analytical approach was used. Correlations were explored between the *differences* in self-reported psychological state and the *differences* in reward responsiveness between the two isolation sessions (iso-total and iso-with-media). Loneliness and boredom were investigated as these state variables showed isolation-induced effects that were significantly different between the two isolation sessions (See Section 2.3.1). For reward seeking, RTs were used¹¹ for high reward-high-effort trials. These trials are considered most relevant for studying motivation and reward seeking (i.e., capturing participants' willingness to expend effort for rewards – see Treadway et al. (2009) for a similar rationale). For reward

¹¹Non-log-transformed RT data were used because recommendations from Gelman and Hill (2006) are for linear models and do not apply to correlations.

Figure 3.3 Reward Learning Task – Optimal Parameters



Note. Using simulations, the optimal combination of learning rate and inverse temperature which predicted highest choice accuracy for the task design used in this study was mapped. The values were obtained from data simulations based on the assigned reward probabilities, task length and frequency of reversals. Bright yellow colouring depicts high choice accuracy while purple colouring indicates low choice accuracy (50% equals chance performance). The yellow area indicates the optimal combination of learning rate and inverse temperature predicting the highest choice accuracy for the present task setup. Higher learning rates and inverse temperature values of > 3 were shown to be optimal.

learning, the focus was on learning rates¹². For both reward seeking and reward learning, correlations were analysed separately for each context/feedback condition (social, nonsocial; Bonferroni corrected $p < .025$ [($.05/2$)]).

3.2.2.4 Software

Data processing, analysis and visualisation were conducted in Python (version: 3.7) using Jupyter Notebook (packages SciPy, Pandas, NumPy and Seaborn). Mixed-effects models were implemented in Matlab 2020a and computational modelling was implemented in RStudio.

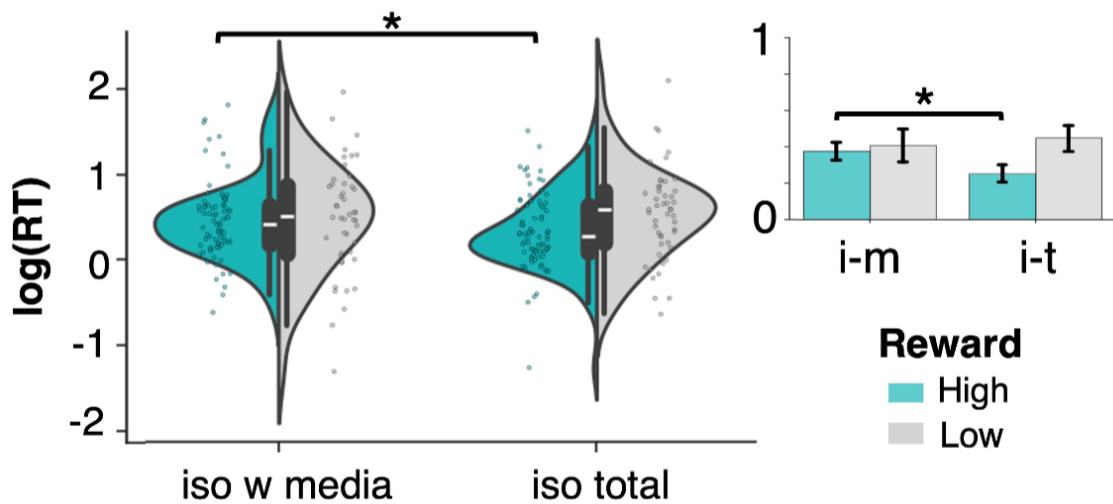
¹²Individual-level parameters were used for this analysis as past work has shown that correlation analyses are not affected by two-step approach bias (Katahira, 2016).

3.3 Results

3.3.1 Reward Seeking

For reward seeking, **choice RTs** showed a three-way interaction between session, reward and context ($b = -0.26$, $t = -3.00$, $p = .003$). Choice RTs were lower in the iso-total compared to the iso-with-media session for high reward trials in the social context across levels of effort (Figure 3.4). Sensitivity analyses provided no evidence that order effects contributed to these results (see the supplement).

Figure 3.4 Reward Seeking – Social Context



Note. Faster response times (RTs) during the reward seeking task following iso-total compared to iso-with-media for high reward trials in the social context (collapsed across levels of effort). Violin plots depict log-transformed response times (RTs) plotted separately for high rewards (green) and low rewards (grey) for the social context. The insert bar plots depict the contrast values for each session: iso-with-media (i-m) and iso-total (i-t), showing the mean for each session. In the plot, the white horizontal lines indicate the median, the bold black vertical lines the interquartile range and the thin black vertical lines the $1.5 \times$ interquartile range minima and maxima. The error bars indicate the standard error of the mean. Lines (with stars) indicate a significant difference ($p < .05$). *Source:* Reproduced from Tomova, L., Towner, E., Thomas, K., Zhang, L., Palminteri, S., & Blakemore, S.-J. (2025). *Communications Psychology*. CC-BY 4.0.

3.3.2 Reward Learning

3.3.2.1 Performance

Reward learning performance was quantified by behavioural measures including choice RT's, accuracy and perseverative errors. For **choice RTs** there was an effect of session (Figure 3.5C), such that across phases and feedback types participants showed faster RTs in the iso-total session compared to baseline ($b = 0.19$, $t = 2.48$, $CI = [0.04, 0.35]$, $p = .013$). For **accuracy** there was an effect of phase (Figure 3.5B), such that across sessions and feedback types participants showed lower accuracy in the first reversal and third reversal phases compared to acquisition (in these phases reward contingencies were opposite from those during acquisition; first reversal $b = -0.11$, $t = -1.98$, $CI = [-0.21, -0.001]$, $p = 0.048$; third reversal $b = -0.20$, $t = -3.67$, $CI = [-0.30, -0.09]$, $p < 0.001$). For **perseverative errors** there was an interaction between session and phase across feedback types, such that for the first reversal phase (Figure 3.5D) participants showed lower perseverative errors in the iso-total session compared to baseline ($b = 0.10$, $t = 2.22$, $CI = [0.01, 0.19]$, $p = 0.026$) and in the iso-total session compared to the iso-with-media session ($b = 0.08$, $t = 2.06$, $CI = [0.004, 0.16]$, $p = .040$). Sensitivity analyses provided no evidence that order effects contributed to these results (see the supplement).

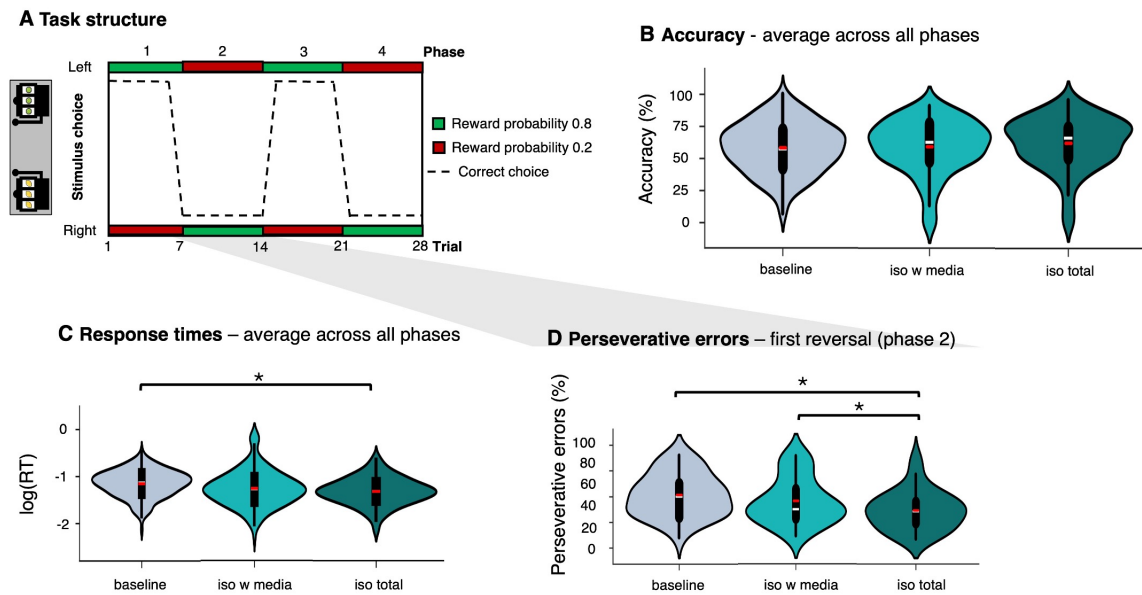
3.3.2.2 Computational Modelling

In addition to behavioural performance, reward learning was quantified using computational modelling to estimate parameters of reinforcement learning. The fictitious update model was found to show the best-fitting results¹³ controlling for model complexity (Table 3.1; see Section 3.2.2.2 for details on model fitting). The model fit of the fictitious model was assessed and validated by running posterior predictive checks and parameter recovery. Parameter recovery was successful, and the model predictions captured the data well (see the supplement for details).

To interrogate the effects of social isolation, hierarchical Bayesian hypothesis testing was used to extract and compare the group-level posterior distribution parameters ($learning_{pos}$, $learning_{neg}$, $beta$) between sessions (baseline, iso-total and iso-with-media) for each feedback type (social, nonsocial). Figure 3.6 depicts the mean posterior distributions for each model parameter (Figure 3.6A) and the difference distributions for each case and parameter of interest (Figure 3.6B).

¹³R-hat values of all models were lower than 1.05 suggesting MCMC samples were well mixed and converged to stationary distributions.

Figure 3.5 Reward Learning – Performance



Note. A) The structure of the task. Feedback was given with an 80 : 20 reward ratio; green blocks indicate high reward (80%) and red blocks low reward (20%). Which stimulus was rewarded was reversed every 7 trials generating 4 phases of the task. B) Average accuracy over the whole task across social and nonsocial conditions shown for each session (baseline, iso with media, iso total). There was no difference in accuracy between sessions. C) Average RTs over the whole task across social and nonsocial conditions for each session. Participants were faster in the iso-total compared to the baseline session. D) Perseverative errors for the first reversal phase (phase 2) across social and nonsocial conditions are shown for each session. Participants made fewer perseverative errors in the iso-total compared to the iso-with-media session and in the iso-total compared to the baseline session. The violin plots illustrate the data distributions for the different conditions. The inserted boxplots illustrate the interquartile range (IQR; box) the white lines signify medians and the red lines signify means. The whiskers extend from the hinge to at most $1.5 \times$ the interquartile range. *Source: Reproduced from Tomova, L., Towner, E., Thomas, K., Zhang, L., Palminteri, S., & Blakemore, S.-J. (2025). Communications Psychology. CC-BY 4.0.*

For interpretation of these results, please see Section 3.2.2.2 for details regarding simulations conducted to determine optimal model parameters for the current task environment. As expected for a short task (28 trials per block) with frequent changes of reward contingencies (every 7 trials; Katahira, 2016), simulations showed that optimal behaviour was characterised by high learning rates (indicating stronger reliance on more recent outcomes for value updating) and lower exploration/higher exploitation (inverse temperature values / $\beta > 3$; Figure 3.3).

Table 3.1 Reward Learning Model Comparison

Model	LOOIC	Bayesian Stacking	Pseudo-BMA	WAIC
RP	6496.026	0.137	0.033	6420.713
EWA	6547.515	0.000	0.000	6445.719
EWA _{rp}	6510.420	0.330	0.025	6418.882
FU	6388.746	0.533	0.942	6315.901

Note. The following model comparison metrics are reported: LOOIC = Leave-One-Out Information Criterion; Bayesian Stacking = stacking of means; Pseudo-BMA = Pseudo Bayesian Model Averaging; WAIC = Widely Applicable Information Criterion. Model abbreviations are as follows: RP = Reward-Punishment Model (model 1); EWA = Experience-Weighted Attraction Model (model 2); EWA_{rp} = Experience-Weighted Attraction Model with separate learning rates for positive and negative prediction errors (model 3); FU = Fictitious Update Model (model 4). For LOOIC and WAIC, lower values indicate better model fit. For Bayesian Stacking and Pseudo-BMA higher values indicate better model fit. The Fictitious Update Model (marked in bold) showed the best model fit. *Source: Reproduced from Tomova, L., Towner, E., Thomas, K., Zhang, L., Palminteri, S., & Blakemore, S.-J. (2025). Communications Psychology. CC-BY 4.0.*

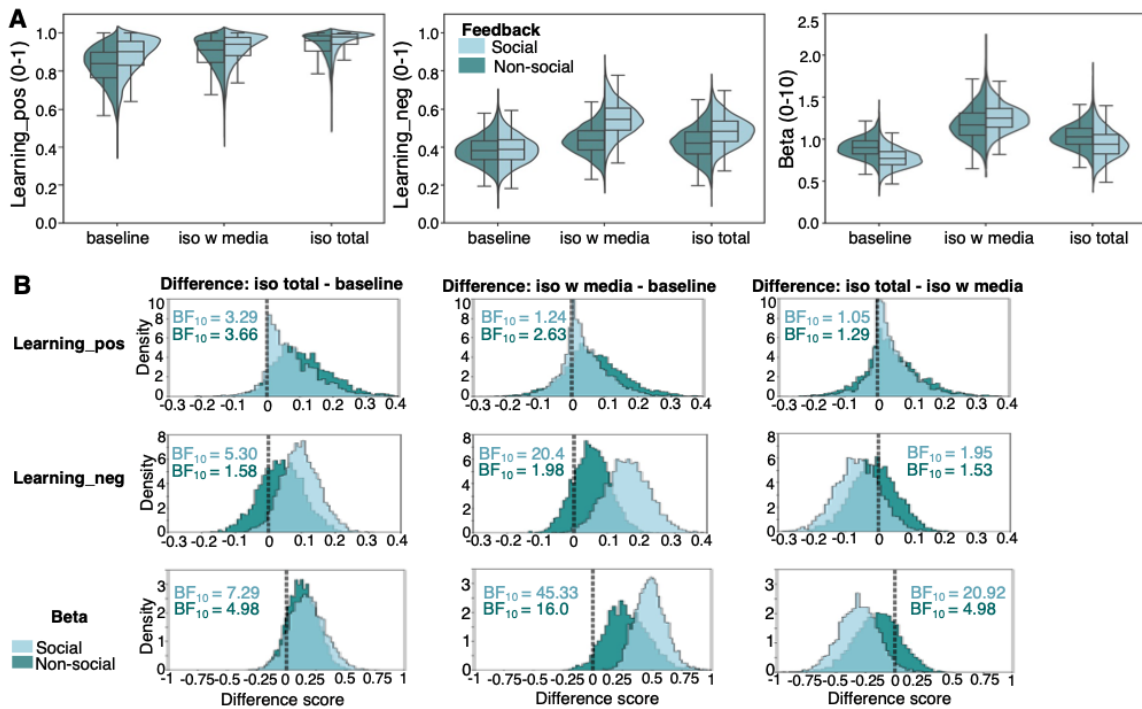
Positive Learning Rate. In the iso-total session compared to baseline, there was a 90% probability for a higher $learning_{pos}$ from social feedback ($BF_{10} = 3.29$) and 93% probability for a higher $learning_{pos}$ from nonsocial feedback ($BF_{10} = 3.66$)

Negative Learning Rate. In the iso-total session compared to baseline, there was a 96% probability for a higher $learning_{neg}$ from social feedback ($BF_{10} = 5.30$)¹⁴. In the iso-with-media session compared to baseline, there was a 99% probability for a higher $learning_{neg}$ from social feedback ($BF_{10} = 20.40$).

Beta. In the iso-total session compared to baseline, there was a 88% probability for a higher $beta$ (indicating less exploration / more exploitation) for social feedback ($BF_{10} = 7.29$) and a 86% probability for a higher $beta$ for non-social feedback ($BF_{10} = 4.98$). In the iso-with-media session compared to baseline, $Beta$ was also higher for both social and nonsocial feedback (social: 100% probability, $BF_{10} = 45.33$; nonsocial: 96% probability, $BF_{10} = 16.0$). In addition, in the iso-total session compared to the iso-with media session, $beta$ was lower for both social and nonsocial feedback (social: 97% probability, $BF_{10} = 20.92$; nonsocial: 78% probability, $BF_{10} = 4.98$).

¹⁴Confirming previous findings (Palminteri et al., 2017), learning rates from positive prediction errors ($learning_{pos}$) were overall higher compared to learning rates from negative prediction errors ($learning_{neg}$).

Figure 3.6 Reward Learning – Computational Modelling



Note. A) Population-level mean posterior distributions of learning rates from positive prediction errors ($learning_{pos}$), learning rates from negative prediction errors ($learning_{neg}$) and inverse temperature ($beta$) for each session for each feedback type. The violin plots illustrate the posterior distributions for the population-level mean effects of the different conditions. The posterior distributions consist of 12,000 samples combined from four Monte Carlo Markov chains. The boxplots illustrate the interquartile range (IQR; box) and the centre lines signify medians. The whiskers extend from the hinge to at most $1.5 \times$ the interquartile range. B) Difference in population-level mean posterior distributions for each pair of sessions (i.e., the difference in iso-total – baseline, iso-with-media – baseline and iso-total – iso-with-media). Plots show the distributions for each feedback type (social, nonsocial). Rows show the difference distributions for each parameter ($learning_{pos}$, $learning_{neg}$ rates and $beta$). The histograms depict the density of difference scores; the dashed lines indicates zero (no difference). The Bayes Factor in support of the alternative hypothesis (BF_{10}) is shown for each pairwise comparison. $BF_{10} > 3$ can be considered as meaningful evidence in support of the alternative hypothesis (that the average difference in posterior distributions for a given comparison is not equal to zero, i.e., evidence of a session effect). *Source: Reproduced from Tomova, L., Towner, E., Thomas, K., Zhang, L., Palminteri, S., & Blakemore, S.-J. (2025). Communications Psychology. CC-BY 4.0.*

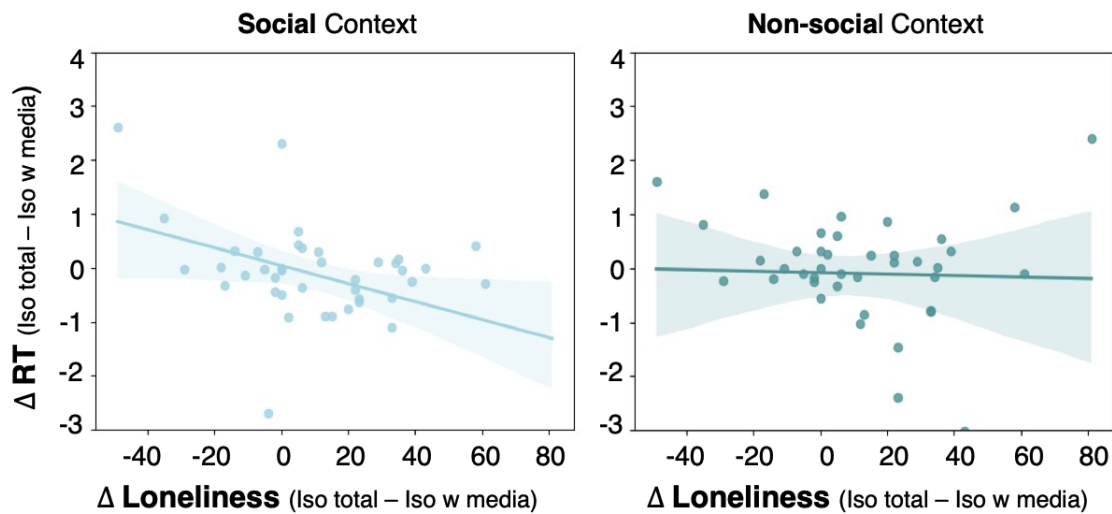
3.3.3 Mechanisms

3.3.3.1 Reward Seeking

In the reward seeking task, a correlation was found between the difference in state loneliness and the difference in choice RTs between the iso-total and iso-with media sessions for the

social context ($r(38) = -0.452$; $p = .003$) but not for the nonsocial context ($r(38) = -0.030$; $p = 0.851$; Figure 3.7). The correlations were significantly different from each other ($z = -1.96$, $p = .025$). Thus, participants who reported higher levels of loneliness after iso-total compared to iso-with-media also showed more social reward seeking after iso-total compared to iso-with-media. There were no associations between reward seeking and the other state variable of interest (boredom).

Figure 3.7 Mechanisms – Reward Seeking



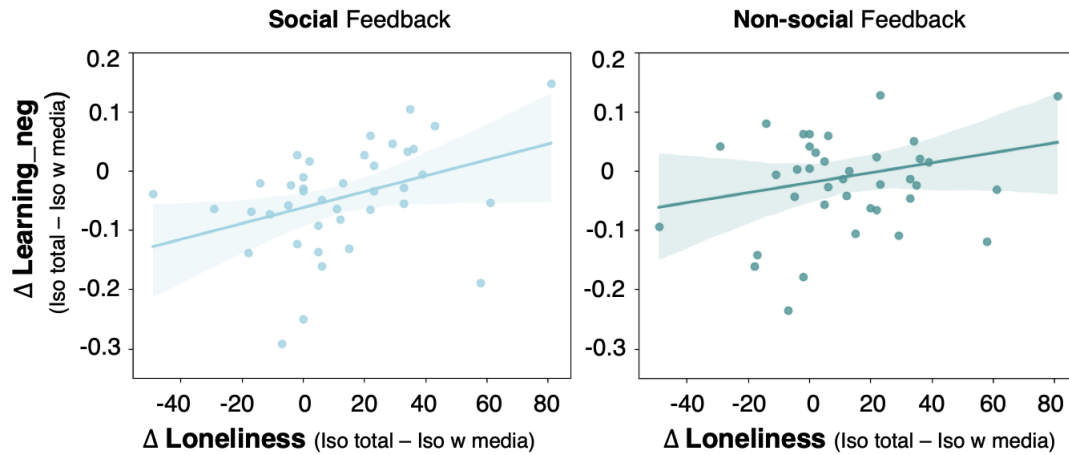
Note. Scatterplots depict the difference between iso-total and iso-with-media in self-reported state loneliness levels and choice RTs during the reward seeking task (high reward, high effort trials) separately for the social and nonsocial context. Individual data points and lines of best fit (with shaded areas depicting the 95% confidence interval) are displayed. The plots show that a stronger increase in state loneliness in the iso-total compared to iso-with-media session was associated with a larger decrease in RTs in the reward seeking task in the social context. *Source: Reproduced from Tomova, L., Towner, E., Thomas, K., Zhang, L., Palminteri, S., & Blakemore, S.-J. (2025). Communications Psychology. CC-BY 4.0.*

3.3.3.2 Reward Learning

For reward learning, a correlation was found between the difference in state loneliness and difference in $learning_{neg}$ rates between the iso-total and iso-with media sessions for the social feedback condition ($r(38) = 0.384$; $p = .015$) but not for the nonsocial feedback condition ($r(38) = 0.222$; $p = .169$; Figure 3.8). However, these correlations were not significantly different from each other ($z = 0.754$, $p = .225$). Thus, participants who reported higher levels of loneliness after iso-total compared to iso-with-media also showed higher reward learning

rates from negative social feedback ($learning_{neg}$). There were no associations between reward learning from negative social feedback ($learning_{neg}$) and the other state variable of interest (boredom). There were no associations between reward learning rates from positive social feedback ($learning_{pos}$) for either loneliness or boredom.

Figure 3.8 Mechanisms – Reward Learning from Negative Feedback



Note. Scatterplots depict the difference between iso-total and iso-with-media in self-reported state loneliness levels and negative learning rates ($learning_{neg}$) from the reward learning task separately for social and nonsocial feedback. Individual data points and lines of best fit (with shaded areas depicting the 95% confidence interval). The plots show that a stronger increase in state loneliness in the iso-total compared to iso-with-media session was associated with a larger increase in negative learning rates ($learning_{neg}$) from social feedback in the reward learning task. *Source: Reproduced from Tomova, L., Towner, E., Thomas, K., Zhang, L., Palminteri, S., & Blakemore, S.-J. (2025). Communications Psychology. CC-BY 4.0.*

3.4 Discussion

Adolescents aged 16 – 19 years, demonstrated increased reward responsiveness, including reward seeking and reward learning, after short-term social isolation. Participants demonstrated evidence of selectively heightened social reward seeking (Shadmehr et al., 2016). After total social isolation, participants were *specifically* faster to decide to expend effort for *large social rewards* compared to after isolation with digital social interactions. Evidence of increased reward learning after social isolation was also found. Participants showed better reward learning performance in the total isolation session compared to baseline and compared to iso-with-media across both social and nonsocial feedback (faster choice RTs in iso-total compared

to baseline and lower perseveration in iso-total compared to baseline and iso-with-media). Participants also showed isolation related improvements in computational parameters of reward learning. Analyses showed that after total isolation (but not after isolation with digital social interactions) participants demonstrated increased reward learning from positive feedback – both social and nonsocial – compared to baseline. With regard to negative feedback, after both isolation sessions compared to baseline, participants demonstrated increased learning from *social* feedback specifically. Further, participants showed more reward exploitation after both isolation sessions compared to baseline for both social and nonsocial feedback. Interestingly, participants exploited rewards more after isolation with digital social interactions compared to total social isolation. Finally, there was a relationship between feelings of loneliness and reward responsiveness for both reward seeking and reward learning. The difference in self-reported state loneliness between the two isolation sessions (which were two highly controlled active conditions) predicted the difference in social but not nonsocial reward seeking. Thus, participants who reported a greater increase in loneliness also showed a larger increase in social reward seeking following total isolation. Further, these two associations were significantly different from each other, suggesting that loneliness might drive social reward seeking specifically. The difference in self-reported state loneliness between the two isolation sessions also predicted the difference in learning rates from negative social but not nonsocial feedback. Thus, participants who reported a greater increase in loneliness also showed a larger increase in learning from negative social feedback following total isolation. However, these two associations were not significantly different from each other and there was no association between loneliness and positive learning rates.

These findings are partially consistent with results from animal models, which have shown that social isolation in adolescent rodents increases reward responsiveness to social, food and drug rewards (Matthews et al., 2016; McCool and Chappell, 2009; Novick et al., 2018). The findings in this chapter suggest that there is a similar effect for reward seeking – at least for social rewards – after total social isolation in adolescent humans. These findings are also in line with human research on chronic loneliness (in adults) showing that individuals high in loneliness show stronger responsiveness to social rewards (Inagaki et al., 2016; Smith and Pollak, 2022; van Roekel et al., 2016). Animal models have also shown that isolation improves learning of stimulus-reward associations (Harmer and Phillips, 1998; Phillips et al., 2002)(but not their reversal [Amitai et al., 2014; Jones et al., 1991; Schrijver et al., 2004]). In line with this, these results suggest that both total social isolation and isolation with digital social interactions improve aspects of reward learning and performance in adolescent humans. In contrast to animal studies, there was some evidence for improved reversal learning after isolation, with participants showing less perseveration after total social isolation compared to both baseline

and isolation with digital social interactions. Participants also showed higher learning rates after isolation, updating associations between cues and rewards throughout the task, particularly in response to social feedback. Thus, these results suggest that, following isolation, adolescents placed more weight on each instance of feedback they received to guide their behaviour, especially when that feedback was social. However, while a high learning rate was optimal in this chapter's task (see Section 3.2.2.2), high learning rates are not always optimal and the interpretation of computational parameters depends on the specific task environment (Zhang et al., 2020a). A high learning rate indicates that participants use the most recent outcomes for value updating, while a low learning rate indicates that both recent outcomes and previous outcomes contribute (Zhang et al., 2020a). Thus, a low learning rate can be optimal in task environments in which reward contingencies are more stable. There was stronger evidence for the effect of isolation on learning from negative social feedback than from positive social feedback. This suggests that following isolation, participants might be hypervigilant towards negative social cues, consistent with findings in Chapter 2. Notably, this effect was stronger in participants who reported greater loneliness after isolation, aligning with research on chronic loneliness (Cacioppo and Hawkley, 2009; Cacioppo et al., 2015).

Higher estimates of inverse temperature (*beta*), indicating greater exploitation and reduced exploration (which was advantageous in this reward learning task described in this chapter), were also found in both isolation sessions compared to baseline. Further, a significant difference in inverse temperature estimates (*beta*) between the iso-total and iso-with-media sessions was observed, with higher values in the iso-with-media condition indicating greater exploitation and reduced exploration. Interestingly, while this was not the only parameter that differed between the isolation sessions, this was the only parameter that showed an iso-with-media relative to iso-total advantage (with respect to optimal parameters for accuracy). However, it is important to note that although lower exploration (higher exploitation) is thought to be adaptive in specific reinforcement learning environments such as this one, higher exploration can be adaptive in other environments (Nussenbaum and Hartley, 2019). It is important to consider how reward learning parameters might lead to adaptive or maladaptive behaviour in everyday life (Zhang et al., 2020a). For example, very high learning rates might lead to an overemphasising of irrelevant features (Zhang et al., 2020a). It should also be noted that while values > 3 were shown to be optimal for this task, participants overall showed low *beta* values, indicating relatively high exploration / low exploitation (Figure 3.6A), with most values ranging between 0.5 – 2 across sessions.

Unlike the the previous chapter (Chapter 2), in addition to differences in reward learning including the inverse temperature (*beta*) parameter, there were also differences in other metrics of reward responsiveness between the two isolation sessions. For example, reward seeking

was heightened in the iso-total session compared to the iso-with-media session. Separately, behavioural reward learning performance was heightened in iso-total compared to both iso-with-media and baseline (as measured by lower perseveration). Therefore, it seems like some aspects of reward responsiveness, compared to threat learning, might be differently affected by access to digital social interactions. These findings could be driven by general effects of digital interactions on attention or motivation. However, inverse temperature (*beta*) was more strongly affected on social feedback trials compared to nonsocial feedback trials suggesting a possible alternative explanation. A substantial number of participants (18 out of 40;45%) reported spending more than 50% of their isolation time participating in digital social interactions. Behaviour on social media platforms has been shown to conform to the principles of reward learning: users space their posts to maximise the average rate of accrued social rewards, considering both the effort cost of posting and the opportunity cost of inaction (Lindström et al., 2021). Thus, a period of intense engagement in digital social interactions might alter the reinforcing nature of other social cues, resulting in altered exploration towards such cues (with subsequent differences in inverse temperature (*beta*) parameters).

Taken together, these findings demonstrate that even brief periods of social isolation can significantly impact reward responsiveness in adolescents, particularly for social rewards. The stronger effects observed following total isolation compared to isolation with digital social interactions suggest that digital social interactions might partially – but not completely – remediate the effects of isolation with regard to reward responsiveness. These results align with theoretical frameworks suggesting that social isolation activates motivational systems to restore social homeostasis (Cacioppo and Cacioppo, 2018; Matthews and Tye, 2019), with increased reward responsiveness potentially serving an adaptive function by motivating reconnection after periods of isolation. However, the heightened sensitivity to negative social feedback following isolation also suggests potential vulnerabilities, particularly for adolescents with pre-existing risk factors such as social anxiety, low self-esteem or a history of peer victimisation. This highlights the importance of individual differences in sensitivity to the effects of social isolation. In the following chapter, I investigate whether individual differences in reward-related brain activity can predict which adolescents are most sensitive to the effects of social isolation on reward responsiveness.

Chapter 4

Neural Predictors of Sensitivity to Social Isolation in Adolescents

4.1 Introduction

In the previous chapter (Chapter 3), I outlined the behavioural effects of social isolation on reward-related behaviour in human adolescents. Animal research has consistently shown that adolescent social isolation affects reward-related brain circuits as well as behaviour. An early study suggested that isolation during adolescence heightened the impact of reward-related stimuli by interacting with dopamine-dependent processes in the nucleus accumbens¹ (NAcc; Jones et al., 1990). Since then, reward-related dopaminergic signalling has become one of the most well-studied systems with regards to adolescent social isolation (Walker et al., 2019). More recently, animal studies have shown that social isolation results in increased dopaminergic response to drug rewards in adolescence compared to other developmental stages (McWain et al., 2022), that social group size during adolescence alters social behaviour and dopaminergic systems (Kim and Lee, 2025) and that social isolation during adolescence alters reward-induced dopamine levels in a brain region-specific manner, with implications for reward-related behaviour (Lallai et al., 2024). In human adults, recent research has shown that reward-related brain regions showed selective responses to social cues after acute social isolation (Tomova et al., 2020).

As discussed in Section 1.4.3, neural activity during reward processing is thought to underlie behavioural changes that characterise adolescence (e.g., risk-taking, reward learning). Many studies have shown that adolescents exhibit a stronger neural response in the ventral striatum during reward processing compared to adults and children. This heightened response has been

¹Substantial evidence has shown that the NAcc regulates reward-related behaviours (Bagot et al., 2015; Bendersky et al., 2021; Winter et al., 2007)

observed across various reward types (Chein et al., 2011; Ernst et al., 2005; Gadassi Polack et al., 2023; Galvan et al., 2006; Galván and McGlennen, 2013; Guyer et al., 2009; Van Leijenhorst et al., 2010). In contrast, other studies have shown weaker adolescent neural responses in the nucleus accumbens (NAcc) during reward processing compared to adults (Bjork et al., 2004, 2010; Vaidya et al., 2013). In addition to these cross-sectional findings, longitudinal studies have found developmental differences in neural reward processing. One study found increased reward-related striatal activation in response to large versus small rewards from the age of 16 – 20 years (Lamm et al., 2014). Another study using a gambling game, found that NAcc activity in response to rewards peaked in adolescence and decreased in young adulthood (Braams et al., 2015). Separately, a study comparing adolescents at two time points (age 14 and age 18) found that neural reward sensitivity was lower in some regions and higher in others (Cao et al., 2021).

Importantly, individual differences in neural reward sensitivity have been correlated with real-world outcomes. For example, reward sensitivity during adolescence has been associated with the emergence of impulsive decisions, risk-taking behaviours and substance use (Jollans et al., 2016; Karoly et al., 2015; Weiland et al., 2013). Sensation seeking has been negatively correlated with reward-related neural activity in adolescents (Cao et al., 2019). Further, individual differences in neural reward sensitivity have been found to predict the development of several adolescent psychiatric disorders, including depression and ADHD (Hoang et al., 2025; Ma et al., 2016; Scheres et al., 2007). Adolescents and adults with depression consistently show altered reward-related brain activity; among individuals with depression, findings suggest diminished responsiveness to monetary rewards in the striatum (Forbes and Dahl, 2012). In adolescents with depression, this reduced striatal reactivity has been observed during decision-making, anticipation and experiencing of outcomes related to monetary rewards (Forbes et al., 2006, 2009).

Finally, neural reward sensitivity has been shown to moderate the associations between behaviour and the social context. In one study (Telzer et al., 2021), adolescents with high reward-related neural sensitivity exhibited increased risky behaviour when they perceived more deviant peer norms. In contrast, adolescents with low neural reward-related sensitivity showed low risk-taking behaviour regardless of peer context, remaining resilient to deviant peer norms. Separately, in the context of diminished in-person social interactions amid the COVID-19 pandemic, a study found that adolescents with higher neural reward sensitivity experienced increased loneliness and social dissatisfaction with more frequent digital social connections with friends, while those with lower neural reward sensitivity showed the opposite effect (Dziura et al., 2023).

4.1.1 Aims

This chapter investigates whether individual differences in neural reward sensitivity might predict the effects of acute social isolation on behavioural reward responsiveness in adolescents. At baseline, neural reward sensitivity was measured using functional magnetic resonance imaging while participants completed a monetary incentive delay task. Here, I focus on the following research question: (Q1) Does reward-related brain activity predict the effects of acute isolation on reward responsiveness? It was hypothesised that participants who showed higher neural sensitivity to rewards would be more sensitive to the effects of isolation in behavioural measures of reward responsiveness (i.e., reward seeking and reward learning).

4.2 Methods

This chapter is a part of the social isolation study described in Chapter 2. Therefore the participants, social isolation procedures and study design in this chapter are identical to those described in Chapter 2. I expand on the neuroimaging procedures below.

4.2.1 Procedures

4.2.1.1 Neuroimaging

During the baseline session, participants underwent functional magnetic resonance imaging (fMRI) to provide a measure of neural reward sensitivity. At the baseline session, magnetic resonance imaging (MRI) data were collected on an ultra-high field 7-Tesla scanner (Siemens 7T Terra) located at the Wolfson Brain Imaging Centre, University of Cambridge. For each participant, an MP2RAGE sequence was used to collect T1-weighted structural images in 224 interleaved sagittal slices with 0.7-mm isotropic voxels (FOV: 224 mm). A field map (phase-difference B0 estimation; echo time 1 (TE1) = 1.11 ms, echo time 2 (TE2) = 3.06 ms) was also collected to control for spatial distortions, which are particularly problematic with ultra-high field scanning (Chaudhari et al., 2009). During acquisition of the anatomical images (approximately seven minutes in total), participants underwent a practice run of a behavioural task. DTI images were also acquired with a scanning protocol of 90 1.4 mm-thick contiguous axial slices with an in-plane resolution of 1.4×1.4 mm providing full brain coverage. Using functional magnetic resonance imaging (fMRI), blood-oxygen-level-dependent (BOLD) signal was measured at a single voxel in successive scans (a voxel time-series). Functional data were collected during four runs of a behavioural task (monetary incentive delay task) to measure neural reward sensitivity (see Section 4.2.2.1 below). Each functional run consisted of 250

volumes with 96 T2*-weighted echo planar slices (TR = 1500 ms, TE = 25 ms, FOV = 192 mm, 128×128 matrix, yielding a voxel size of $1.5 \times 1.5 \times 1.5 \text{ mm}^3$) acquired as a partial-head volume in an anteroposterior phase-encoding direction using interleaved slices. The functional scans took approximately 25 minutes in total.

4.2.2 Measures

4.2.2.1 Monetary Incentive Delay Task

At baseline, a monetary incentive delay task (MID; Knutson et al., 2000) was used to measure **neural reward sensitivity**. The MID task is a well-established task used to study neural correlates of reward anticipation (i.e., winning money). During the task, participants were able to win either £0.2 (small win) or £5 (large win), or lose £0.2 (small loss), or £5 (large loss). On some trials, participants did not win or lose any money, which served as control trials. On each trial, participants were first presented with a cue indicating whether they could win or lose money on that trial. The cue was a yellow star with the amount of the possible win or loss written inside (i.e., 0 [control trials], 0.2 [small win trials], 5 [large win trials], -0.2 [small loss trials], -5 [large loss trials]). Following the cue, participants saw a white circle on the screen presented for a jittered time interval (range 1.5 – 4 s, $M = 2.5$ s) briefly followed by a white square, which was presented for 100 ms and then the circle again. Participants' task was to press a button as fast as possible when they saw the square. Following their response, participants were presented with feedback revealing whether they were successful or not on that trial (won or avoided a loss; presented for 500 ms). At the end of each trial participants saw a fixation cross for a jittered time interval (range 2 – 6 s, $M = 3.5$ s) before the next trial began. The task was adaptive and the time window for how fast participants needed to respond narrowed or widened depending on their response times during the task to ensure that participants won on most (approximately 80%) of the trials (to keep the task rewarding) but also that the task was not too easy (to keep participants engaged). Participants underwent a practice run of the task during the anatomical MP2RAGE scan, and the data from this run was used to calibrate the initial response window for the MID task.

4.2.3 Data Analysis

4.2.3.1 Neural Reward Sensitivity

Preprocessing. Functional MRI data were preprocessed using the pipeline implemented in Tomova et al. (2020), apart from the MP2RAGE processing described below. The nipy and nipyne (Gorgolewski et al., 2011) open source preprocessing pipelines were used for fMRI

data. First, the `heudiconv` python application was used to convert data into the NIFTI image file format using `dcm2niix`, and then to organise that data into a BIDS-formatted directory structure. `fMRIPrep` (Esteban et al., 2019) was used to minimally preprocess the anatomical and functional data (using default settings but including susceptibility distortion correction using `fieldmaps`). Because the fMRI data was collected on 7T and an MP2RAGE sequence was used, which is not a format that is currently supported by `fMRIPrep`, the MP2RAGE data was first processed so it could be used by `fMRIPrep`. To this end, an offline reconstruction method was applied using in-house code that reconstructs a phase-sensitive inversion recovery (PSIR) image from MP2RAGE scans (nifti files). The PSIR file was then added as a T1 file into `fMRIPrep` to be processed and was treated as a T1 anatomical scan in `fMRIPrep`. Using `fMRIPrep`, anatomical images were skull-stripped: the atlas-based ANTS program (Tustison et al., 2014) was used first and then skull-stripping was refined using information from FreeSurfer surfaces after reconstruction was completed (Dale et al., 1999). The FMRIB Software Library (FSL) FAST program (Zhang et al., 2001) was used for brain tissue segmentation. Images were spatially normalised to MNI-space using ANTS (using the multiscale, mutual-information based, nonlinear registration scheme). Brain masks, tissue segmentation and FreeSurfer surfaces were visually inspected for quality control. Phase-difference B0 estimation (Jezzard and Balaban, 1995) was used for susceptibility distortion correction. A reference image for each run was generated from the input BOLD timeseries. A functional brain mask was created using a combination of FSL, ANTS, AFNI and `nilearn` tools (Abraham et al., 2014). FSL's MCFLIRT program (Jenkinson et al., 2002) was used to estimate and correct for head motion, which generated a coregistered BOLD series and motion-based confound regressors. Additional confound regressors were generated, including other measures of motion (framewise displacement and DVARS and anatomical CompCor [Behzadi et al., 2007] timeseries derived from cerebrospinal fluid [CSF] and white matter tissue segments). FreeSurfer's program "bbregister" (Greve and Fischl, 2009) was used to align the reference image of each run with the anatomical image. The timepoint-to-functional reference transformation, the functional reference to anatomical transformation, and the anatomical-to-MNI transformation were concatenated into a single transformation and used to transform each functional timeseries into MNI template space. The preprocessed timeseries for run-level analyses was assessed with algorithms from the Artifact Removal Toolbox (ART) to identify frames within each run that had an abnormal amount of motion (0.4 mm of total displacement, or an intensity spike greater than three standard deviations from mean). Any run containing a framewise displacement greater than 0.4 mm on more than 25% of the total frames was excluded from additional analyses. Based on these criteria, one run from one participant which showed a framewise displacement (FD) of 0.42 had to be removed. All other runs were within the movement limit (across participants, across runs

$M_{FD} = 0.17$, $SD = 0.06$, range = 0.08 – 0.33). FSL's SUSAN tool (Smith and Brady, 1997) was used for spatial smoothing with a 6 mm smoothing kernel. The tool uses segmentation boundaries to avoid smoothing across tissue types. We used MRIQC, an open-source quality assurance software tool (Esteban et al., 2017), to generate additional reports which display Image Quality Metrics (IQMs).

Regions of Interest. To analyse the functional data from the MID task, whole brain analyses and region of interest (ROI) analyses were applied. Whole brain data was used to generate group-level contrasts for the high reward versus no reward conditions to assess whether the resulting group-level brain activation was in line with expected activation for this contrast (Oldham et al., 2018). For the ROI analyses, regions that have been consistently activated during reward anticipation in an Activation Likelihood Estimation meta-analysis of 50 fMRI studies using the MID task were included (Oldham et al., 2018). These regions comprised: the ventral striatum (VS), midbrain (MB), amygdala (AMY), anterior insula (AI), occipital cortex (OC), thalamus (TH) and supplementary motor area (SMA). ROIs were created using the Harvard–Oxford cortical and subcortical probabilistic anatomical atlases; included in FSL. It was not possible to find an anatomical mask for the anterior insula and therefore ROIs were created based on peak activation locations reported in Oldham (2018; left AI: $-40, 14, -8$; right AI: $34, 24, -2$). Five millimetre spheres were drawn around these peak coordinates and a binary mask combining left and right AI was created. For these ROI's, neural reward sensitivity was quantified using both univariate and multivariate methods.

Modelling. The nipy framework (Gorgolewski et al., 2011) was used to conduct the analyses. The design matrix included boxcars for the experimental conditions convolved with a double-gamma hemodynamic response function (HRF), and nuisance regressors representing frame-wise motion, the anatomical CompCor regressors derived from white matter and CSF, as well as impulse regressors for volumes identified by ART. A high-pass filter was applied to the design matrix and the smoothed data. The model was evaluated using FSL's FILM (Jenkinson et al., 2012). Participant-level contrast maps were generated using FSL's FLAME (Jenkinson et al., 2012) in mixed-effects mode. Both univariate and multivariate measures of neural reward sensitivity were assessed, as outlined below.

Univariate. Mean activation from the contrast high reward > no reward during the anticipation phase of the MID task was extracted as a measure of univariate neural reward sensitivity from each ROI (7 ROIs in total).

Multivariate. Multivariate analyses have been suggested to detect differences between conditions with higher sensitivity than conventional univariate analyses (Davis et al., 2014). A multivariate measure of neural reward sensitivity was also employed by quantifying the similarity of the multivariate spatial patterns of activity between high reward versus no reward during the anticipation phase of the MID task from each ROI. Multivariate classification accuracy here can be seen as an indication of the amount of information about a variable of interest available in the BOLD signal (Jehee et al., 2011; Kok et al., 2012), such that individual differences in classification accuracy indicate neural reward sensitivity in the multivariate domain. Differences between multivariate and univariate approaches do not afford conclusions about the nature or dimensionality of the neural signal (as both can also stem from the same source [Davis et al., 2014]). Thus, here, these measures were used to assess the same concept (i.e., neural reward sensitivity) and were corrected for multiple comparisons across the different measures (see Section 4.2.3.1 below). All multivariate analyses were conducted with the PyMVPA toolbox (Hanke et al., 2009) in Python and Matlab 2020a.

For each ROI for each participant, the β values from the generalised linear model (that is, the amplitude of the fitted HRF) of the response to the two conditions of interest (high reward, no reward) for each trial in each run (28 trials per condition per run 4 runs) were extracted, resulting in 112 β values for each voxel. Responses were extracted from all voxels in the anatomically identified ROIs in each participant. No additional feature selection was applied. A machine learning algorithm was trained to decode neural patterns of high reward versus no reward for each participant within each ROI. A 4-fold linear support vector machine (SVM; using linear kernel) classification was used for which the classifier was trained on 3 of the runs from the MID task while one run was left out for testing. This was done 4 times (4-folds) so that each run was a testing data set on one of the folds. Classification accuracies from each fold were then averaged to create a measure of classification accuracy for each ROI for each participant. To obtain confidence intervals of the mean classification accuracy for each ROI, bootstrapping was used. One thousand datasets were generated randomly by sampling with replacement from the classification accuracies for each ROI across participants using Matlab's `bootci` function.

Analyses. While the selected ROIs were chosen based on highly consistent univariate responsiveness to the MID task across different studies, they might not necessarily also represent reward anticipation in the multivariate domain. Therefore, it was first tested whether these multivariate classification accuracies for each ROI across participants were significantly above chance, indicating the ability to decode high reward versus no reward representations in that ROI. For hypothesis testing at the group level, a permutation analysis following the methods in

Stelzer et al. (2013) was used. This nonparametric approach does not depend on assumptions about the distribution of classification accuracies (Allefeld et al., 2016; Stelzer et al., 2013). A null distribution was generated from the data (Stelzer et al., 2013). The condition labels were shuffled randomly during training within each run, and then the same 4-fold cross-validation approach was used to obtain prediction accuracies for each fold, which were then averaged to create a measure of classification accuracy for each ROI for each participant. This permutation analysis was performed 100 times per participant (thus creating 100 random permutations), resulting in 100 accuracy values per participant. To create a null distribution at the group level, one of the 100 accuracy values for each participant was then randomly drawn and a mean across participants was calculated. This procedure was repeated 10^5 times for each ROI, creating the null distributions for each ROI. The probability of obtaining a mean accuracy value in the null distributions that is equal to or higher than the true mean from the analyses was calculated. The null hypothesis (no group-level decoding) was rejected if $p < .001$ (Stelzer et al., 2013).

To investigate individual differences in reward-related sensitivity to social isolation, Pearson correlation analyses were conducted between both univariate and multivariate measures of neural reward sensitivity and behavioural measures of reward responsiveness (reward seeking and reward learning rates) in both the baseline and iso-total sessions. For these analysis, reward seeking was quantified as RTs from the high reward / high effort conditions (mean across nature and social contexts; see Chapter 3). Separate correlations for each ROI for each measure of neural reward sensitivity (univariate and multivariate; 14 tests in total) were calculated and results were reported as significant at $p < .003$ ($0.05/14$). ROI data analysis² and visualisation was implemented in Python (version: 3.7) using Jupyter notebooks (using packages PyMVPA, SciPy, Pandas, NumPy and Seaborn) and Matlab2020a.

4.3 Results

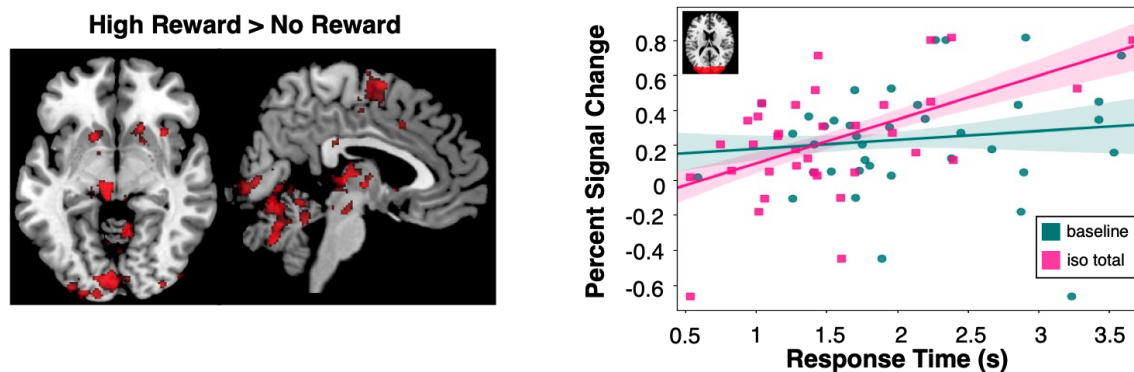
4.3.1 Neural Reward Sensitivity

At the group level, high reward versus no reward representations were successfully decoded in all of the 7 selected ROIs: VS (mean accuracy= 0.57, bootstrapped CI= [0.54, 0.59], $p < .001$); MB (mean accuracy= 0.55, bootstrapped CI= [0.53, 0.58], $p < .001$); OC (mean accuracy= 0.58, bootstrapped CI= [0.55, 0.61], $p < .001$); AI (mean accuracy= 0.55, bootstrapped CI= [0.52, 0.57], $p < .001$); TH (mean accuracy= 0.56, bootstrapped CI= [0.53, 0.59], $p < .001$); SMA (mean accuracy= 0.57, bootstrapped CI= [0.54, 0.60], $p < .001$); AMY (mean accuracy= 0.51, bootstrapped CI= [0.48, 0.53], $p < .001$). The left panel of Figure 4.1 shows

²All statistical tests reported were performed two-tailed.

the group level results from the task (contrast high-reward > no-reward anticipation), which revealed activity in reward-related regions, as expected (Oldham et al., 2018). The classification accuracy obtained from each participant from the SVM classification was used as a measure of multivariate neural reward sensitivity for subsequent analyses.

Figure 4.1 Neural Reward Sensitivity



Note. Left) Univariate group level activity family-wise error (FWE) corrected at the voxel level ($p < 0.05$) for the contrast High Reward > No Reward during the anticipation phase of the MID task. *Right)* Brain reward signals predicting reward seeking after isolation (iso-total) but not at baseline for univariate neural reward signals in occipital cortex. Plots depict individual data points, regression lines and confidence intervals (standard errors of the estimate) between neural reward signals and RTs in the reward seeking task in the baseline (blue) and iso-total (pink) session.

Individual level univariate neural reward sensitivity in the occipital cortex showed a significant correlation with RTs in the reward seeking task in the iso-total session ($r(38) = 0.54$, $p < .001$; right panel of Figure 4.1). This association was not present at baseline ($r(38) = -0.12$, $p = .465$; baseline and iso-total correlations differed significantly from each other: $z = 2.08$, $p = .038$), suggesting that neural reward sensitivity in this region predicted reward seeking following social isolation. Multivariate neural reward sensitivity did not predict reward seeking for any of the ROIs (all values $p > .300$). Neural reward sensitivity (univariate and multivariate) did not predict learning rates in the reward learning task for any of the ROIs (all values $p > .030$).

4.4 Discussion

The preliminary evidence presented here found that neural reward sensitivity predicted some individual differences in the effects of isolation on reward seeking. Adolescents with lower neural reward sensitivity in the occipital cortex at baseline showed increased reward

seeking after total isolation compared to baseline. Interestingly, the direction of the observed effect was contrary to the hypothesis. Prior research has shown associations between *heightened* neural reward sensitivity and increased propensity for social risk taking (Telzer et al., 2021) and increased loneliness and social dissatisfaction amid the COVID-19 pandemic (Dziura et al., 2023). However, the findings in this chapter are not inconsistent with evidence showing opposite associations, with some studies finding *decreased* neural reward sensitivity predictive of increased vulnerability. For example, one study showed a link between *lower* neural reward-related activity and higher sensation seeking in adolescents (Cao et al., 2019). Separately, another study showed that in young adults (aged 18 – 26 years) lower neural reward sensitivity predicted less resilience to stress (Hu et al., 2022).

Of the seven preregistered ROIs investigated, only the occipital cortex showed an association with reward seeking post-isolation in this study. While the occipital cortex is responsible for processing visual information, it has been identified in meta-analyses as one of the core brain regions consistently activated during reward anticipation in the MID task (Oldham et al., 2018) and in other monetary reward tasks (Jauhar et al., 2021). Interestingly, the occipital cortex has also been implicated in the neurobiology of loneliness according to a recent systematic review (Lam et al., 2021). Studies have found associations between loneliness and primary and secondary visual cortex in terms of volume (Kiesow et al., 2020), functional connectivity (Mwilambwe-Tshilobo et al., 2019), causal flow (Tian et al., 2016) or activation to social images (Cacioppo and Hawkley, 2009; Wong et al., 2019). Given that the high reward and no reward condition in the MID task used in this study did not differ visually, except for the number presented inside the star ("0" in the no reward condition and "5" in the high reward condition), the measured brain activity might represent a neural signal of visual attention and processing of reward-predictive cues (Frank and Sabatinelli, 2019; Krebs et al., 2012; Ress et al., 2000). The extent to which individuals sense and perceive rewards might shape how strongly they are affected by social isolation. Because social interactions are themselves rewarding (particularly for adolescents; Cann et al., 2020; Ethridge and Weinberg, 2018; Nardou et al., 2019), those who perceive rewards less robustly at baseline might require greater amounts of social contact to feel socially fulfilled. As a result, they may have been more impacted by the short-term social isolation in this experiment, leading to a heightened drive for reward-seeking post-isolation. In contrast, individuals with higher baseline reward perception might have been less affected by the relative deprivation of social rewards following a brief period of social isolation.

The findings in this chapter suggest that *lower* neural reward sensitivity as indicated by univariate activity in the occipital cortex at baseline might indicate greater vulnerability to the effects social isolation. Critically, this association was specific to reward-seeking following isolation. However, it is important to note that this finding might be specific to the effects

of social isolation on reward-related behaviour. Those with *higher* neural reward sensitivity might be, in contrast, more vulnerable to the effects of social isolation in other domains, such as feelings of loneliness or threat processing. Conceptually, low responsiveness to rewards has been linked to anhedonia and might represent a marker of vulnerability with regard to the effects of social isolation on mental health disorders such as depression (Nikolova et al., 2012; Southwick et al., 2005; Vidal-Ribas et al., 2019). Increased reward seeking might also put adolescents at risk for substance use and abuse, particularly when social connections are reinstated. As discussed in the previous chapter (Chapter 3), synergistic effects of social and drug rewards have been observed, with social reward amplifying the reinforcing properties of drugs in adolescent rats (Reyna et al., 2021). In humans, studies consistently show that adolescents are significantly more likely to use substances such as alcohol, tobacco and cannabis when in the company of friends and that peer influence is one of the strongest predictors of adolescent drug use. Identifying individual differences in susceptibility to social isolation could help predict which adolescents are most at risk and inform targeted interventions tailored to the symptoms they are most likely to develop based on their unique neural profiles.

Part II

Chapter 5

The Role of Online and Offline Self-Disclosure for Social Connection

A version of this chapter has been published:

Towner, E., Grint, J., Levy, T., Blakemore, S.-J., & Tomova, L. (2022a). Revealing the self in a digital world: A systematic review of adolescent online and offline self-disclosure. *Current Opinion in Psychology*, 45(101309). DOI: 10.1016/j.copsyc.2022.101309

5.1 Introduction

Building upon the empirical findings from Part I, which investigated the effects of acute social isolation, identified neural predictors of sensitivity to isolation and examined whether digital social interactions can mitigate isolation-induced effects, Part II employs nonexperimental methods to further explore these questions. This first chapter in Part II investigates self-disclosure, a key component for social bonding, by comparing the effectiveness of online versus offline self-disclosure in fulfilling adolescent social needs. "Self-disclosure", in which an individual reveals personal information to another (Ignatius and Kokkonen, 2007; Pearce and Sharp, 1973), is an important building block for relationships (Derlega and Chaikin, 1976). Self-disclosure is thought to help form and maintain social relationships as it builds trust between individuals (Altman and Taylor, 1973). An early meta-analysis suggested that people who self-disclose tend to be more liked, and that people like those to whom they self-disclose (Collins and Miller, 1994). In addition, it has been proposed that self-disclosure is inherently rewarding in that people are willing to forgo money in order to disclose information about themselves (Tamir and Mitchell, 2012; Tamir et al., 2015).

However, self-disclosure might manifest differently in digital versus face-to-face interactions. Some studies suggest that the ability to engage in selective self-presentation online might increase self-disclosure (Walther et al., 2001). Others propose the lack of non-verbal cues in computer-mediated communication may lead to decreased self-disclosure (Joinson, 2001). Similarly, while online self-disclosure can help to build trust within a relationship (Rheingold, 2000; Walther, 1996), it has been proposed that self-disclosure conducted via computer-mediated communication is less fulfilling than face-to-face self-disclosure (Lee et al., 2011).

This systematic review investigates two separate, but related, research questions: (Q1) How is self-disclosure important for relationship-building in adolescence?; and (Q2) Is this different for online and offline communication? The primary aim of this systematic review was to ascertain the ways in which self-disclosure is important for building social relationships, and thus can fulfil social needs, in adolescence. This involved identifying the appropriate recent literature and identifying key themes relating to factors that affect self-disclosure and the impact it has on social relationships. From there, a comparison was sought between the efficacy of online communication and offline interaction in the fulfilment of these social needs. Online communication offers fewer nonverbal cues (such as facial expressions in text-based messaging) and higher anonymity (Lieberman and Schroeder, 2020) and therefore differs from face-to-face interactions in substantial ways. Previous research in adults has shown mixed findings regarding the amount of self-disclosure in online versus offline contexts (Nguyen et al., 2012). Given that adolescents spend more time than adults socialising via digital means (Bayindir and Paisley, 2019), it was hypothesised that self-disclosure in social interactions in adolescents would be affected differently by online communication versus offline communication.

5.2 Methods

For this systematic review, the PRISMA guidelines were followed (Liberati et al., 2009). This review was preregistered¹ on the Open Science Framework.

5.2.1 Procedure

5.2.1.1 Search Strategy and Inclusion Criteria

The SCOPUS database was searched for papers published between 2010 and 2021, which were related to the use of self-disclosure in adolescence in both offline and online communication. To achieve this, the following search terms were used: (TITLE-ABS-KEY (((adolescen*

¹DOI: 10.17605/osf.io/q57gc

OR teen*) AND ("self-disclosure" OR "informing others" OR "social sharing") AND (virtual OR "computer-mediated" OR online)) OR ((adolescen* OR teen*) AND ("self-disclosure" OR "informing others" OR "social sharing")) AND "social" AND (PUBYEAR> 2009)) AND NOT ("clinical").

The inclusion criteria meant that, whether the study was conducted online or offline, only papers that studied self-disclosure in a social context among 10 – 24-year-olds were included in the final review. Further, papers published before 2010 were excluded, to ensure recent findings that potentially involved online communication were being discussed. Papers that discussed self-disclosure in a clinical or familial setting, or that assessed self-disclosure as a personality trait, were also excluded. Finally, reviews and empirical papers that included qualitative data only were excluded.

5.2.1.2 Data Extraction and Analysis

Two independent reviewers searched and screened the literature. 218 studies were retrieved from the SCOPUS database. It was determined that 38 of these studies were potentially relevant and needed to be read in full to test their eligibility. Overall, 19 studies were included in the final review based on the predetermined inclusion and exclusion criteria. Papers were excluded for: (1) having an incompatible age range of participants (i.e., outside of 10 – 24 years); (2) being focused on relationships other than those among peers; (3) studying personality traits rather than social relationships; (4) being a review rather than an empirical study; or (5) having a qualitative design.

Of the 19 studies, 5 (26%) included samples from the U.S., a further 8 studies (42%) included European samples (based in the Netherlands, Belgium, Germany, Sweden or Turkey), and the final 6 studies (32%) were conducted in Asian countries (Taiwan, Malaysia, China and Singapore). The age range of participants across studies was 10 – 22 years and all studies were quantitative by design and used self-report measures of self-disclosure. In 7 studies (37%), the authors had developed their own measure of self-disclosure; this was more common among the studies that were measuring online self-disclosure, where established measures are yet to be developed.

5.2.1.3 Quality Assessment

Methodological and reporting quality of each record included in the systematic review was assessed using an adapted version of the Downs and Black Checklist (Downs and Black, 1998). The original checklist was adapted to suit the non-interventional nature of the research question. Two reviewers (ET and TL) critically appraised each study and sum scores were converted into

percentages. Notes regarding critical appraisal were kept and major disagreements between co-reviewers were resolved by a third reviewer (LT). After resolving major disagreements, interrater reliability was assessed. The intraclass correlation coefficient (ICC) estimate and its 95% confidence interval was calculated using R package irr (Gamer et al., 2019), based on a mean-rating ($k = 2$), consistency, 2-way mixed-effects model. The ICC was 0.76 with a 95% confidence interval from 0.37 to 0.91 ($F(18, 18) = 4.09, p = .002$), indicating good reliability. For each study, the two reviewer scores were averaged; mean quality assessment scores are reported in Table 5.1. The adapted checklist, quality assessments and other materials can be found in the supplement.

Table 5.1 Self-Disclosure – Study Summary

Source		
Schug et al. (2010)	Method	A new scale developed by combining the Self-Disclosure Scale (Miller, Berg, and Archer, 1983) and the psychological component of the Enomoto Self-Disclosure Scale (Enomoto, 1997).
	Sample	<i>Study 1</i> : Japanese sample: 74 (32 female); American sample: 93 (72 female). <i>Study 2</i> : Japanese sample: 94 (29 female).
	Location	Japan and U.S.
	Age	<i>Study 1</i> : Japanese Participants: $M = 18.98$ ($SD = 0.88$); American Participants: $M = 19.18$ ($SD = 2.13$). <i>Study 2</i> : $M = 18.90$ ($SD = 0.66$)
	Setting	Offline
	Findings	A gender difference was reported, showing females self-disclose more than males. Even controlling for this gender difference, individuals reported engaging in higher levels of self-disclosure to strengthen their relationships with their peers.

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Source

	Quality Score	$M = 76$ ($SD = 5.53$)
Schiffrin et al. (2010)	Method	Self-disclosure was measured via the Self-Disclosure Scale (SDS; Miller, Berg, & Archer, 1983). A modified version of the SDS was used to measure online self-disclosure.
	Sample	99 (71 female)
	Location	U.S.
	Age	$M = 19.00$ ($SD = 1.11$)
	Setting	Both online and offline
	Findings	The study showed that participants were more likely to disclose intimate information in face-to-face interactions than computer mediated communication. Both forms of self-disclosure were positively correlated with subjective well-being.
	Quality Score	$M = 62$ ($SD = 4.16$)
Valkenburg et al. (2011)	Method	Self-disclosure was measured using the Online Intimate Self-Disclosure Scale (Schouten et al., 2007) which is an adapted version of the Self-Disclosure Scale (Miller, Berg, & Archer, 1983).
	Sample	690 (345 female)
	Location	The Netherlands

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Source

	Age	Participants divided into 4 age groups: 10–11-year-olds: $n = 182$, $M = 10.57$ ($SD = 0.56$); 12–13-year-olds: $n = 166$, $M = 12.54$ ($SD = 0.61$); 14–15-year-olds: $n = 179$, $M = 14.54$ ($SD = 0.55$); 16–17-year-olds: $n = 163$, $M = 16.51$ ($SD = 0.50$)
	Setting	Both online and offline
	Findings	Gender differences were reported for adolescent self-disclosure behavior. It was shown that both online and offline self-disclosure increased quickly between ages 10–13 years for females before plateauing, whereas this same trajectory was found later for their male counterparts (ages 12–15 years). 26% of participants showed a preference for online disclosure than offline. More boys were in this group than girls – particularly boys in early adolescence (12–13 years old) of which 40% preferred online compared to offline disclosure.
	Quality Score	$M = 85$ ($SD = 7.64$)
Courtois et al. (2012)	Method	Self-Disclosure was measured using a five-item measure obtained from Parks and Floyd (1996).
	Sample	352 (246 female)
	Location	Belgium
	Age	$M = 16.44$ ($SD = 1.39$)
	Setting	Both online and offline

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Source

	Findings	The results suggest that adolescents use computer mediated communication to learn information about their peers, something which is deemed important for establishing offline friendships, partly because it encourages self-disclosure. This was shown to be particularly important for anxious adolescents.
	Quality Score	$M = 79$ ($SD = 6.36$)
Huang and Yang (2013)	Method	Modified Leung's (2002) "Self-disclosure when chatting on ICQ" to develop a Self-Disclosure Scale for real life and cyberspace.
	Sample	608 (407 female)
	Location	Taiwan
	Age	Range: 13–18 years (no further age information provided)
	Setting	Both online and offline
	Findings	The authors found a negative correlation between accurate face-to-face self-disclosure and online misrepresentation. Adolescents who were more truthful in real-life self-disclosure engaged less in online misrepresentations.
	Quality Score	$M = 71$ ($SD = 5.26$)
Koutamanis et al. (2013)	Method	Online Self-Disclosure was measured using the Online Intimate Self-Disclosure Scale (Schouten, Valkenburg and Peter's, 2007).
	Sample	690 (345 female)
	Location	The Netherlands

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Source

	Age	At first wave - Range: 10–17 years, $M = 13.42$ ($SD = 2.27$)
	Setting	Both online and offline
	Findings	The authors found that use of instant messaging was positively correlated with self-disclosure and the initiation of offline friendships.
	Quality Score	$M = 77$ ($SD = 5.97$)
Almquist et al. (2014)	Method	Data was derived from a survey within the larger "Individual Life Chances in Social Context" study which included measures of self-disclosure.
	Sample	1289 (642 female)
	Location	Sweden
	Age	All participants were born in the year 1990. Data were collected between October 2009 and January 2010
	Setting	Offline
	Findings	A gender difference was found, showing that females engage in self-disclosure more than their male counterparts; however, self-disclosure was positively related to being in friendship in males.
	Quality Score	$M = 68$ ($SD = 4.83$)
Salı and Akyol (2014)	Method	The Peer Relationship Scale was used as a measure of self-disclosure.
	Sample	1390 (534 female)
	Location	Turkey

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Source

	Age	Range: 15–17 years (no further age information provided)
	Setting	Offline
	Findings	The authors reported a gender difference, regardless of whether children worked or not, that females engaged more in self-disclosure than males.
	Quality Score	$M = 65$ ($SD = 4.35$)
Liu and Brown (2014)	Method	Items from the Self-Disclosure Scale (Miller, Berg, & Archer, 1983) were adapted for the context of online communication.
	Sample	264 (186 female)
	Location	China
	Age	$M = 19.2$ years (no information on SD provided)
	Setting	Online
	Findings	Adolescent online self-disclosure was significantly correlated with bridging social capital, an individual's network through which they can access resources such as social support, even when an individual's social status and gender were controlled for. Boys disclosed more demographic information (e.g., birth date, hometown, contact information, etc.) about themselves than girls.
	Quality Score	$M = 73$ ($SD = 5.45$)

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Source

Liu (2014)	Method	A survey questionnaire with three sections was used to obtain data. The items for self-disclosure were based on work by Derlega, Metts, Petronio, and Margulis (1993).
	Sample	1370 (no gender information provided)
	Location	Taiwan
	Age	Range: 11–14 years (no further information provided)
	Setting	Online
	Findings	The study found that as closeness of Facebook friends' increases, the amount of self-disclosure intimacy, and trust also increases. Additionally, the amount of self-disclosure predicts the level of intimacy with Facebook friends.
	Quality Score	$M = 69$ ($SD = 4.92$)
Krcmar et al. (2015)	Method	Online self-disclosure was measured using the Online Intimate Self-Disclosure Scale (Schouten et al., 2007).
	Sample	381 (188 female)
	Location	The Netherlands
	Age	$M = 15.64$ ($SD = 2.54$)
	Setting	Online

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Source

	Findings	Male participants reported more self-disclosure than female participants. Self-disclosure was positively associated with the personality traits narcissism and egocentrism, though this association was stronger for egocentrism. Imaginary audience ideation (i.e., the assumption that others are looking at and thinking about oneself almost all times [Elkind, 1978]) is related to increased self-disclosure behaviours on Facebook.
	Quality Score	$M = 74$ ($SD = 5.65$)
Ang et al. (2015)	Method	Online self-disclosure was measured using the Online Intimate Self-Disclosure Scale (Schouten et al., 2007).
	Sample	1572 (899 female)
	Location	Malaysia
	Age	$M = 15.05$ ($SD = 1.08$)
	Setting	Online
	Findings	Certain aspects of computer mediated communication (i.e., attitude towards online relationship formation) acted as predictors for online self-disclosure and the satisfaction of psychological needs in online friendships. When these needs were met, online friendships could also predict life satisfaction.
	Quality Score	$M = 78$ ($SD = 6.17$)

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Source

Xie and Kang (2015)	Method	Data was taken from the Teens and Privacy Management Survey, with there being 10 items specifically for measuring self-disclosure.
	Sample	622 (318 female)
	Location	U.S.
	Age	$M = 14.94$ ($SD = 1.60$)
	Setting	Online
	Findings	Self-disclosure of adolescents was shown to be positively predicted by the level of trust between them and their peers, the number of Facebook friends they had and the amount of time they spent actively on social media. Boys disclosed more personal contact information than girls.
	Quality Score	$M = 81$ ($SD = 6.75$)
Liu et al. (2016a)	Method	A 14-item Likert scale was used to measure textual self-disclosure; a similar 8-item measure was used for visual disclosure.
	Sample	780 (397 female)
	Location	Singapore
	Age	$M = 13.94$ ($SD = 0.90$)
	Setting	Online
	Findings	The authors found a positive correlation between textual and visual adolescent self-disclosure and narcissism. The authors also report a gender difference in textual disclosure but not visual.

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Source

	Quality Score	<i>M</i> = 72 (<i>SD</i> = 5.37)
Liu et al. (2016b)	Method	Self-disclosure was assessed via a revised version of the Online Intimate Self-Disclosure Scale (Schouten et al., 2007).
	Sample	296 (175 female)
	Location	China
	Age	<i>M</i> = 16.9 (<i>SD</i> = 1.36)
	Setting	Online
	Findings	Exhibitionism, as a personality variable, was found to mediate a relationship between need satisfaction and online adolescent self-disclosure.
	Quality Score	<i>M</i> = 75 (<i>SD</i> = 5.72)
Ashktorab et al. (2017)	Method	Self-disclosure was assessed using self-developed questions.
	Sample	243 (85 female)
	Location	U.S.
	Age	<i>M</i> = 19.6 (<i>SD</i> = 0.82)
	Setting	Online
	Findings	The results indicated that more self-disclosure leads to better relationship quality between adolescents and also elicits greater social support.
	Quality Score	<i>M</i> = 70 (<i>SD</i> = 5.11)

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Source

von Salisch (2018)	Method	Attitudes towards self-disclosure were measured using the "Selbstoeffnung". This is a 4-item self-report measure used previously by Roehrle (1994).
	Sample	299 (148 female)
	Location	Germany
	Age	$M = 12.6$ ($SD = 0.57$)
	Setting	Offline
	Findings	Increased self-disclosure among adolescents was related to more reciprocal friendships and more meaningful disclosure over time. It was also suggested that individuals who are depressed are more prone to socially isolate themselves and less likely to disclose intimate information. Girls were shown to engage more in self-disclosure than boys.
	Quality Score	$M = 82$ ($SD = 6.87$)
Viktorovna et al. (2019)	Method	The authors developed a questionnaire that included items on self-disclosure behaviours in social media.
	Sample	62 (26 female)
	Location	Russia
	Age	Range: 15–20 years (no further age information provided)
	Setting	Online

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Source		
	Findings	The type of online self-disclosure was shown to vary with gender, with females being more likely to promote ideas or photos than males. Females also scored higher in trait self-blame, which, like introversion, was negatively associated with online self-disclosure – adolescent males were less likely to self-disclose online than adolescent females.
	Quality Score	$M = 67$ ($SD = 4.73$)
Vijayakumar et al. (2020)	Method	Self-disclosure was measured using the Shulman’s Self-Disclosure Scale (Shulman et al, 1997). The value was of self-disclosure was measured as the monetary reward that participants would forgo to disclose the information.
	Sample	125 (all female)
	Location	U.S.
	Age	$M = 11.55$ ($SD = 0.81$)
	Setting	Offline
	Findings	Self-disclosure was shown as inherently rewarding, as adolescents would willingly forgo monetary rewards in favour of self-disclosure; it was suggested that this is because self-disclosure would help build trust and improve their relationship quality with their peers. Adolescents preferred superficial self-disclosure over intimate self-disclosure and particularly girls with high self-esteem engaged more in superficial self-disclosure.

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Source

Quality Score $M = 84$ ($SD = 7.37$)

Note. This table summarises the empirical studies included in this systematic review which examine self-disclosure behaviours among adolescents in both online and offline settings. Quality Assessment Scores range from 0–100 ($M = 73.53$ ($SD = 6.97$)). *Source:* Reproduced from *Current Opinion in Psychology*, Volume 45, Towner, E., Grint, J., Levy, T., Blakemore, S.-J., & Tomova, L. (2022a) *Revealing the self in a digital world: A systematic review of adolescent online and offline self-disclosure*. Copyright (2022) Elsevier.

5.3 Results

5.3.1 Relationship Building

Twelve (63%) of the studies included in the review explored the association between relationship quality and adolescent self-disclosure. All of these studies proposed that adolescent self-disclosure improves relationship quality as it builds trust between peers (Almquist et al., 2014; Courtois et al., 2012; Day et al., 2007; Hsiung Liu, 2014; Koutamanis et al., 2013; Liu and Brown, 2014; Richards et al., 2015; Sail and Akyol, 2010; Schiffrin et al., 2010; Schug et al., 2010; Vijayakumar et al., 2020; von Salisch, 2018; Xie and Kang, 2015). For adolescents, self-disclosure indicates a commitment to the peer and to the relationship with the peer (Sail and Akyol, 2010), strengthening it and leading to more reciprocal friendships (von Salisch, 2018). Two papers expanded upon this, suggesting that self-disclosure improves relationship quality because it creates a way to build social support (Ashktorab et al., 2017; Liu and Brown, 2014). Overall, results suggest that self-disclosure improves relationship quality among adolescents.

Furthermore, all reviewed papers highlight a positive relationship between psychological well-being and adolescent self-disclosure. Two papers (Ang et al., 2015; Liu et al., 2016b) showed that adolescent self-disclosure predicts psychological needs satisfaction, and, in turn, life satisfaction. One paper suggested this may be because adolescents find self-disclosure to be a rewarding activity (Vijayakumar et al., 2020), and so engaging in it has positive effects for wellbeing (especially for males; Almquist et al., 2014). Other possible explanations for the link between wellbeing and self-disclosure include the notion that it allows individuals to explore and form their own identity (Viktorovna et al., 2019), a key part of adolescent development

(Pfeifer and Berkman, 2018). A bidirectional relationship was identified here, suggesting that those with higher psychological wellbeing engage in more self-disclosure (von Salisch, 2018).

5.3.2 Online versus Offline

Of the papers included in the final review, 9 (48%) of them investigated online adolescent self-disclosure, 5 (26%) investigated offline communication, and the final 5 (26%) compared the two. Findings suggest that, while the frequency of both online and offline self-disclosures was linked to better relationship quality (Ashktorab et al., 2017; Liu and Brown, 2014; Xie and Kang, 2015), adolescents showed a preference for face-to-face communication (Schiffrin et al., 2010). Nevertheless, there was evidence that online self-disclosure is a useful tool for bridging social capital, especially during significant life transitions (Liu and Brown, 2014) and for practising the social skills required for face-to-face communication (Courtois et al., 2012; Huang and Yang, 2013; Koutamanis et al., 2013; Valkenburg and Peter, 2011).

More specifically, three studies found that online self-disclosure provides unique benefits for the fulfilment of adolescents' social needs. Koutamanis et al. (2013) looked at how adolescents' online social behaviour influences their ability to initiate offline friendships. This study used a longitudinal design measuring the use of instant messaging, participants' ability to initiate offline friendships, diversity of the groups of people who participants communicated with online and online self-disclosure behaviour. Instant messaging was positively associated with participants' ability to initiate offline friendships. The researchers posited that this might be due to the increased diversity of the people they were able to communicate with online positively influencing the initiation of offline friendships. Courtois et al. (2012) looked at how learning information from another person's online profile affects in-person relationships and communication by using questionnaires on online uncertainty reduction, level of certainty, self-disclosure and social anxiety. They found that particularly for individuals who scored high on a social anxiety scale (Social Interaction Anxiety Scale [SIAS]; Mattick and Clarke, 1998) looking at online profiles can provide information about what people are like offline, which can alleviate social anxiety. Valkenburg et al. (2011) used a longitudinal design to assess intimate online and offline self-disclosure using questionnaire measures. All participants used online self-disclosure to improve offline communication skills, demonstrating how online self-disclosure influences offline self-disclosure.

5.3.3 Moderators

It was also explored whether the literature identifies moderating factors in the effects of self-disclosure such as gender and type of disclosure. Overall, five studies found that female

adolescents self-disclosed more than male adolescents (Almquist et al., 2014; Sail and Akyol, 2010; Schug et al., 2010; Viktorovna et al., 2019; von Salisch, 2018). Female adolescents may have been reported as self-disclosing more as they begin doing so from a younger age and their friendship networks were defined by self-disclosure and commitment to their peers, unlike male friendship networks (Almquist et al., 2014). In contrast to this, two papers found higher self-disclosure in males than in females Krcmar et al. (2015); Liu and Brown (2014) while three papers did not find significant gender differences (Huang and Yang, 2013; Koutamanis et al., 2013; Liu et al., 2016b). One study reported a gender difference in text-based self-disclosure, but did not report whether disclosure was higher in males or females (Liu et al., 2016a). Interestingly, one longitudinal study found that particularly young boys (12 – 13-year-olds) preferred online compared to offline self-disclosure and that this effect disappeared after age 13 when boys showed a sharp increase in offline self-disclosure (Valkenburg et al., 2011). In addition, two studies found that boys disclose more demographic (e.g., birth date, home town) and contact information online than girls (Liu and Brown, 2014; von Salisch, 2018).

While the observed effects of self-disclosure (such as an association with higher relationship quality) were found across different measures of self-disclosure (see Table 5.1 for details), few studies directly compared effects of different types of self-disclosure outside of comparing online versus offline self-disclosure. One study compared the effects of superficial to intimate self-disclosure in adolescent girls and found that girls preferred to self-disclose superficial information about themselves rather than intimate information – an effect that was higher in girls with high self-esteem (Vijayakumar et al., 2020). The authors found that while sharing intimate information was undertaken with caution by all participants, particularly girls with high self-esteem showed a strong preference to share superficial information about themselves.

Almost none of the reviewed studies reported any negative effects of self-disclosure except for one (Xie and Kang, 2015) that assessed regret about online self-disclosure. The authors found that particularly teens who use social network sites (SNS) more frequently and have more SNS friends (particularly unfamiliar friends) report regret about online postings more often.

In sum, this systematic review found that self-disclosure is an important component for adolescents in building relationships. Furthermore, the results supported the hypothesis that there are differences between online and offline self-disclosure. Findings suggest that online self-disclosure is less fulfilling compared to offline self-disclosure. However, certain populations, such as highly anxious young people and young boys aged 12 – 13 years, appear to benefit more from online self-disclosure than offline self-disclosure.

5.4 Discussion

The first research question in this chapter asked how self-disclosure affects relationship-building in adolescence. This systematic review showed that self-disclosure is an important tool for building trust and showing commitment, as well as improving psychological wellbeing in young people aged 10 – 22 years. The second research question asked how self-disclosure differs in online compared to face-to-face social interactions. A recent review identified core features of online social interactions that distinguish them from face-to-face communication (Lieberman and Schroeder, 2020): They provide fewer nonverbal cues (such as facial expressions in text-based messaging), higher anonymity, more opportunity to form new social ties across geographical distances and wider possibilities of dissemination of information (i.e., a social media post can reach thousands of people in a short amount of time, which is difficult in face-to-face interactions). Thus, online social interactions differ from face-to-face interactions in substantial ways. While they offer opportunities for socialising that are not possible in face-to-face interactions (such as interactions across geographical distances and reaching a high number of people in short time) they also represent a more limited way of interacting with others (by lacking nonverbal cues and having higher anonymity).

Online self-disclosure appears to be less fulfilling and beneficial for relationship quality than face-to-face self-disclosure. However, the results of this systematic review also indicate that online self-disclosure can be beneficial for highly anxious young people as it allows them to seek out more information about their peers, thus reducing their uncertainty around a relationship. More specifically, adolescents with higher levels of anxiety were shown to engage more in gathering information about friends on social networking sites (for example, by viewing their online profiles), which in turn mediated the negative relationship between social anxiety and levels of certainty about a friendship. This indicates that online self-disclosure can be helpful for young people with high social anxiety.

This review also showed gender differences in adolescent self-disclosure. Despite inconsistent results of the impact that gender may have on adolescent self-disclosure, several studies suggested that female adolescents engage in self-disclosure more than male adolescents. Previous research suggested that this gender difference in self-disclosure occurs, partly because of differences in the assumed gender stereotypes in society (Jourard, 1971). It is often assumed that females engage in more self-disclosure than males because they are more "socially oriented" (Hwang et al., 2015) while the ideal of male toughness and stoicism may be able to predict difficulties in self-disclosing (especially personal information; (Bruch, 2002)). Societal gender stereotypes might explain gender differences in adolescent social behaviour as adolescents are only starting to form their own identity, with their actions largely guided by

what they have seen in wider society already. Surprisingly, some studies showed that the gender difference observed for offline self-disclosure are reversed in the online world –here males tend to disclose more, particularly when it comes to demographic and contact information. In line with this, a longitudinal study showed that young boys aged 12 – 13 years preferred online self-disclosure compared to face-to-face self-disclosure which then stimulated offline self-disclosure after the age of 13 in these boys (Valkenburg et al., 2011). The authors found support for a "rehearsal hypothesis" in their data meaning that adolescents use the internet as a relatively safe place where they can rehearse their self-disclosure and self-presentation skills (e.g., Valkenburg and Peter, 2008, 2009). This finding is intriguing as it suggests a unique role of online social interactions in the development of social skills for young boys.

These results also support Altman and Taylor's (1973) Social Penetration Theory, which provides an explanation for the role of self-disclosure in the formation and maintenance of interpersonal relationships. Altman and Taylor proposed that social relationships develop in quality as self-disclosure brings breadth and depth to the relationship and increases trust between the individuals. An alternative explanation is provided by uncertainty reduction theory (Berger and Calabrese, 1975), which suggests that people self-disclose and seek disclosure from others to reduce uncertainty at any point in their relationships. Such an account also considers the reciprocal nature of relationships and might explain the finding from our systematic review that online self-disclosure was overall seen as less fulfilling than face-to-face self-disclosure. There is, in general, more uncertainty during online self-disclosure due to the added anonymity and lack of nonverbal cues in online communications, and therefore self-disclosure during online interactions might be less successful in reducing uncertainty in relationships. However, for young people who find social interactions threatening or have less experience with them, face-to-face self-disclosure might not carry these beneficial features, while online self-disclosure might provide a safer way to engage with others. This in turn might help certain young people (such as people who are very anxious and young boys aged 12 – 13 years) to strengthen their face-to-face relationships.

Overall, this chapter suggests that self-disclosure is important in fulfilling adolescent social needs as it improves interpersonal relationship quality (by building trust) and individual psychological well-being. This review also showed that online self-disclosure is less successful in fulfilling adolescent social needs although certain populations (such as young people with high anxiety and young boys) might benefit more from online self disclosure. These findings are relevant in contexts where in-person socialising is not possible – such as amid social distancing measures in response to the COVID-19 pandemic. Many young people were compelled to socialise with peers mainly – or exclusively – via social media during this period. Indeed, studies (Newlove-Delgado et al., 2021) reported that 13.8% of adolescents (aged 17 – 22 years)

often or always felt lonely as a result of COVID-19 pandemic-related lockdowns and other restrictions on socialising. Thus, online social interactions might provide unique ways to deal with such restrictions on face-to-face social interactions and help promote feelings of connectedness in young people. The next chapter investigates this more directly, exploring whether digital social interactions might mitigate loneliness in the context of the COVID-19 pandemic which severely restricted in-person social contact.

Chapter 6

Loneliness and Digital Social Interactions during COVID-19

A version of this chapter has been published:

Towner, E., Tomova, L., Ladensack, D., Chu, K., & Callaghan, B. 2022b. Virtual social interaction and loneliness among emerging adults amid the COVID-19 pandemic. *Current Research in Ecological and Social Psychology*, 3(100058). DOI: 10.1016/j.cresp.2022.100058

6.1 Introduction

As described in Section 1.7, modern technology has drastically changed the way we socialise and communicate, facilitating real-time digital social interactions such as messaging, voice and video calling, gaming and social media exchanges (Smith and Anderson, 2018). While the capacity for social connection in this way has expanded possibilities for social contact, whether digital social interactions provide the same opportunity for connectedness as real-life social interactions remains a critical question. As social interactions occur more frequently (and sometimes exclusively) online, it is important to understand whether digital interactions satisfy our need for social connection and mitigate loneliness. Further, when physical proximity is impossible, or ill advised, as was the case during social distancing recommendations amid the COVID-19 pandemic, did digital social interactions help combat loneliness and promote mental health?

Some types of digital social interactions are clearly problematic – such as cyberbullying and participation in groups promoting dangerous pro-anorexia content and self-injury behaviours (Kowalski et al., 2019; Margherita and Gargiulo, 2018). However, other digital social interac-

tions can be positive – for example online support groups for those with depression (Breuer and Barker, 2015). Studies investigating the quality of digital social interactions (including Facebook usage, online gaming and online dating) have shown that they can be similar in meaning, intimacy, and stability as real-life relationships (Ellison et al., 2007; Hsu et al., 2011; Parks and Roberts, 1998; Whitty, 2008). In line with such findings, some researchers have found a positive relationship between Facebook use and the maintenance and creation of social capital (such as employment opportunities, community interaction, and finding new friends and emotional support; Ellison et al., 2007; Hsu et al., 2011). In an experimental study, digital social interactions (anonymous online chats) were shown to reduce loneliness in university students (Shaw and Gant, 2002). Further, online peer support groups have been shown to reduce feelings of isolation (Prescott et al., 2020) and serve as a digital meeting place to practice social skills for use offline (Smit et al., 2021). However, passive social media use (defined as monitoring of other people's lives without direct exchange) has been found to be associated with social comparisons, envy, and lower subjective wellbeing (Verduyn et al., 2017). Time spent on Facebook has also been associated with increased loneliness in young adults (Lou et al., 2012). In another study, experimentally manipulating social media abstinence did not affect self-reported loneliness, wellbeing or quality of day (Hall et al., 2021).

Meaningful social connections are particularly important during specific stages of development, particularly adolescence, as discussed in Section 1.2. Other researchers have posited a redefinition of the period between an individual's late teens through twenties as a unique stage of adolescence called "emerging adulthood" (Arnett, 2000, 2011; Hochberg and Konner, 2019). As societal expectations have shifted, more individuals spend a longer period navigating and exploring peer relationships, continuing their education, and starting their careers in this emerging adulthood period (Sawyer et al., 2018), and digital social interactions become increasingly important at this time too (Thayer and Ray, 2006). In contrast to childhood and early adolescence (when digital social interactions are conducted primarily with existing friends), research has shown that emerging adults are more likely to forge new social connections online, communicating with both friends and strangers (Thayer and Ray, 2006).

The mandated social-distancing measures occasioned by the arrival of the novel coronavirus (COVID-19) around the globe, reduced in-person social interactions for many people and, at least for a time, moved much social contact into the digital domain. Early reports on "lockdown loneliness" during the COVID-19 pandemic lockdowns revealed that emerging adults reported increases in loneliness after the onset of COVID-19 (Shah et al., 2020). Nearly half (44%) of young adults (18 – 24 years old) in the United Kingdom reported feeling lonely during lockdown (compared to only 16% before the lockdown; Mental Health Foundation 2020). Loneliness also increased during COVID-19 in samples of young adults in the United States

(Lisitsa et al., 2020), Switzerland (Elmer et al., 2020), and Canada (Hamza et al., 2021). Initial research showed that increased digital social interactions (including meetings over Zoom, phone calls, texts, virtual gaming, or other similar means of communication that did not involve in-person interaction) with close others amid the pandemic were related to higher levels of wellbeing in both younger ($M_{age} = 20.54$) and older ($M_{age} = 59.15$) adults (Brown and Greenfield, 2021; Sahi et al., 2021b).

In this chapter, I investigate changes in digital social interactions (across a variety of platforms), objective in-person social isolation (number of in-person social contacts), depression, happiness and social needs in emerging adults amid the initial onset of the COVID-19 pandemic. I also sought to identify if a higher frequency of digital social interactions during the pandemic protected against loneliness in this group. Finally, whether digital social interactions were associated with emerging adults' reported happiness and depressive symptoms was explored.

6.2 Methods

6.2.1 Participants

One-hundred and twenty six individuals participated in this COVID study (102 female; 24 male, $M_{age} = 20.54$; $SD = 2.46$; range = 18 – 29 years). Thirty-four participants reported their race/ethnicity as Caucasian, 32 as East Asian, 13 as South Asian, 22 as Latinx/Hispanic, 10 as Middle Eastern and six as African. Eight participants reported their race/ethnicity as "other", and one participant did not report their race/ethnicity. Most participants resided in the United States ($n = 118$). For the analyses discussed in this chapter, participants over the age of 25 were excluded, leaving a final sample of $n = 119$.

6.2.2 Procedure

The data for this study were collected as part of a larger survey study which investigated the relationship between physical and emotional symptoms and health amid the initial onset of the COVID-19 pandemic and social distancing mandates. This study was conducted in collaboration with researchers from the University of California, Los Angeles (UCLA). Data collection for this study commenced on the 28th of April 2020 and concluded on the 4th of June 2020. At the time of data collection, most participants were under a stay-at-home order (as mandated by the state of California). Participants were recruited both using the UCLA Psychology Department Subject Pool (SONA), as well as from the public using advertisements posted on social media platforms such as Twitter, Instagram and Facebook. Participants had

to be 18 years or older to enrol. The protocol for this study was approved by the UCLA institutional review board and participating individuals provided online consent for study participation.

Study data were collected and managed using REDCap (Research Electronic Data Capture; Harris et al. 2019, 2009) hosted at UCLA. Participants completed the survey online and participation was anonymous. The current study considers a subset of the questionnaires (those pertaining to social interactions, loneliness, depression, happiness and social needs) from the larger study. This study was preregistered¹ on the Open Science Framework. Deidentified data and materials are available in the supplement.

6.2.3 Measures

6.2.3.1 Questionnaires

Digital Social Interaction. Digital social interaction (DSI) frequency, feelings of connection, number of practices, and primary practice were assessed using the Adolescent Social Connection and Coping during COVID-19 questionnaire (ASC; Pfeifer 2020). Frequency of digital social interaction was measured on a 7-point scale from "Never" to "Almost constantly". Feelings of connection derived from digital social interaction were measured on a seven-point scale from "Very socially disconnected" to "Very socially connected". Practices, referred to in communication research as "affordances" (Evans et al., 2017), were defined as methods used for digital social interaction and included messaging/texting, voice calls, video calls, social media, online gaming, and any "other" method (which could be typed into a text box). Number of practices was calculated by taking a sum of the methods used. In the same question, participants were also asked to indicate their primary practice. Participants were asked about each of these components in reference to four domains: with 1) friends, 2) acquaintances, 3) family members, and 4) romantic partners, both retrospectively (in a typical two-week period before the onset of COVID-19) as well as currently (in the past two weeks during COVID-19). For the purposes of this paper, results are reported from the domain of "friends" as peer relationships are particularly important for emerging adults (Khullar et al., 2021)(results from other domains can be found in the supplement).

Objective In-Person Social Isolation. Objective levels of in-person social isolation were assessed in three ways: (1) household size, (2) social distancing compliance, and (3) frequency of in-person contact with friends (even if socially distanced). Household size was measured by participants' self-reported number of persons in their household (during COVID-19). Social

¹DOI: 10.17605/osf.io/sw4kp

distancing compliance was assessed by a single question asking participants how often they had been social distancing on a five-point scale. Frequency of in-person contact with friends within the last two weeks was measured on a seven-point scale from "never" to "almost constantly". Over 95% of participants reported social distancing "often" or "always" and over 87% of participants reported seeing friends in-person less than once a week amid the pandemic. As levels of social distancing were high, in-person social contact with friends was low (particularly compared to retrospectively reported pre-pandemic levels of in-person social contact with friends, $M_{before} = 3.38$, $SD_{before} = 1.42$, $M_{during} = 0.92$, $SD_{during} = 1.37$, $t(117) = 15.24$, $p < .001$), and variability between participants on these two variables was low, these variables were not considered further, using only household size as a measure of objective in-person social isolation.

Loneliness. Loneliness was measured using the UCLA Loneliness Scale (Russell et al., 1978), which is a composite measure of both social and emotional loneliness. Participants were asked to report how they felt in the last two-week period (i.e., during COVID-19).

Depression. The Beck Depression Inventory II was used to measure depression (Beck et al., 1996). Participants were asked to report how they felt in the last two-week period (i.e., during COVID-19) as well as retrospectively for a typical two-week period before the onset of COVID-19.

Happiness. Happiness was assessed in two ways, current happiness and change in happiness. First, current happiness was assessed using a modified version of the Subjective Happiness Scale (Lyubomirsky and Lepper, 1999). Here, participants were presented with four statements and/or questions and were asked to indicate the point on the scale they felt was most descriptive of them over the last two weeks during COVID-19. The original Subjective Happiness Scale is presented in a 7-point Likert format, with higher scores representing greater happiness. To have a more fine-grained measure of happiness in this study, participants were instead shown a sliding scale which corresponded to a continuous scale from 0 – 100 for each item. For the purpose of comparing participants' current happiness scores to previous research, each of the four items was converted to a seven-point scale using the equation: $(\text{raw score}/100) \times 6 + 1$. The fine-grained scale was used in all other analyses. Second, change in happiness was assessed by asking participants to rate how their general level of happiness had changed since the onset of COVID-19 (on a five-point scale anchored with the statements "much less happy" to "much happier"). Participants ratings on this scale were called "happiness change".

Social Needs. Participants rated how well their friends met their social needs (from "not at all" to "extremely well" on a 5-point scale), both in the last two weeks (since the onset of COVID-19), and in a typical two-week period before the onset of COVID-19.

Covariates.

Age. Participants reported their age in years.

Sex / Gender. Participants were asked to indicate their sex (male, female or other – with a text box to describe) and gender (woman, man or other – with a text box to describe). No participants in this study selected the other option and all participants gender corresponded to their reported sex.

6.2.4 Hypotheses

It was hypothesised that amid the initial onset of COVID-19, frequency of digital social interactions (DSI) would be negatively associated with loneliness. In addition to this preregistered hypothesis, changes in digital social interactions, objective in-person social isolation, depression, happiness and the fulfilment of social needs were analysed. Associations between digital social interactions and wellbeing (happiness and depression) were also explored.

6.2.5 Data Analysis

6.2.5.1 Post Pandemic Changes

To determine if there were any pre- (retrospective) to post- COVID-19 onset (current) changes in DSI-frequency, DSI-feelings of connection, objective in-person social isolation (persons in household), depression, and whether social needs were being met, a series of paired samples *t*-tests using Bonferroni correction for multiple comparisons (6 *t*-tests in total) with adjusted alpha levels of .008 (.05/6) were performed. To investigate changes in the distribution of DSI primary practice pre- to post- COVID-19 onset and household composition, nominal symmetry tests were conducted (Cohen, 1988). Finally, a one-sample *t*-test with a Bonferroni correction for multiple comparisons with adjusted alpha levels of .008 (.05/6) was used to investigate whether participants rating of happiness change were significantly different than zero, which represented "no change".

6.2.5.2 Pre Pandemic Comparisons

To determine if the sample was exhibiting comparable levels of loneliness, depression and happiness to other samples of emerging adults (assessed before the onset of COVID-19), mean scores from these measures in the sample were compared with those reported in past work (Beck et al., 1996; Lyubomirsky and Lepper, 1999; Russell, 1996) using independent samples *t*-tests with Bonferroni correction for multiple comparisons (3 *t*-tests in total) with adjusted alpha levels of .017 (.05/3).

6.2.5.3 Loneliness, Depression and Happiness

To understand how objective in-person social isolation and digital social interactions during COVID-19 were associated with participants' ratings of loneliness amid COVID-19, a multiple linear regression was conducted. Household size (our measure of objective in-person social isolation) and our four measures of DSI (frequency, feelings of connection, number of practices, and primary practice) were entered into the model as predictors. Age and sex were included as covariates. Participant loneliness during COVID-19 was entered as the outcome of interest.

Because loneliness was not elevated in this sample during COVID-19 compared to a pre-pandemic sample (contrary to expectations), two measures that did show elevation (depression and happiness) were used as additional outcome variables in exploratory analyses. The same multiple linear regression (discussed above) was run but using depression and happiness (instead of loneliness) as outcomes of interest. As three outcomes of interest were investigated (loneliness, depression and happiness) a conservative Bonferroni correction was used for multiple comparisons and the adjusted alpha level was .017 (.05/3).

6.2.6 Other

For loneliness, depression and happiness, a proration was calculated for missing values, up to 30%. Proration was calculated by imputing each participant's missing scores with the mean of their observed scores (mean imputation). Results were similar when calculated with and without mean imputation (results without mean imputation can be found in the supplement). Regression analyses were performed with listwise deletion. R was used for all analyses (R Core Team, 2019). A complete list of all R-packages and versions used can be found in the supplement.

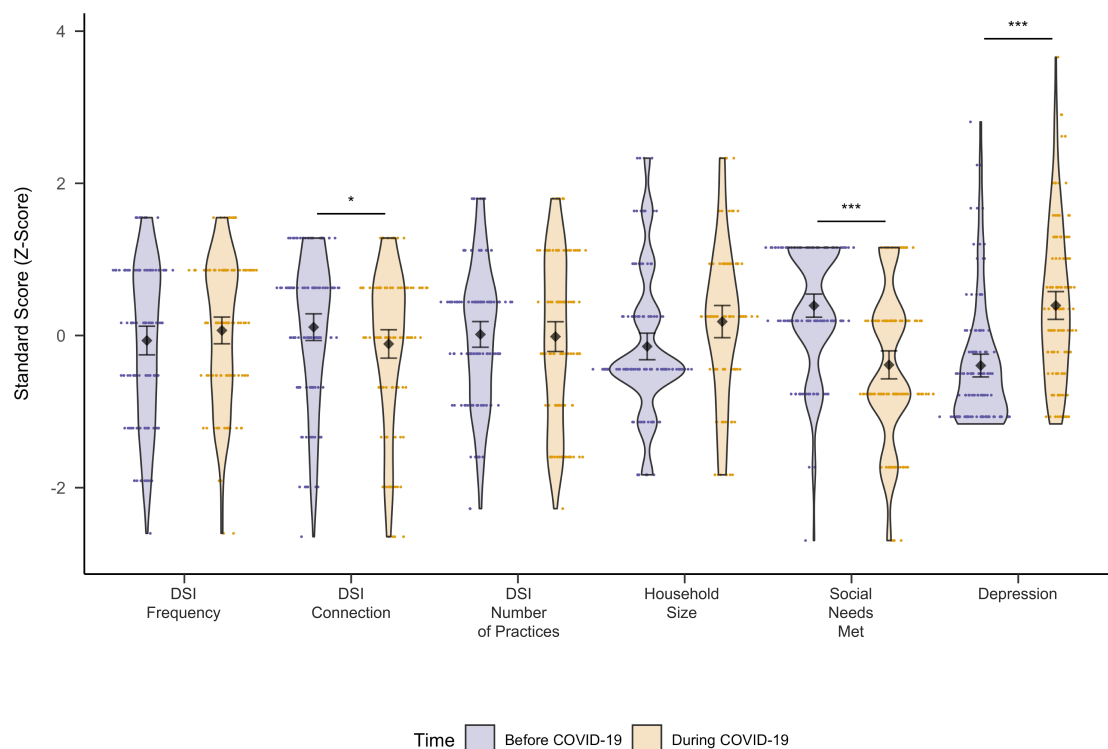
6.3 Results

6.3.1 Post Pandemic Changes

Participants rated their total frequency of engagement in digital social interactions with friends as "about once a day" before and during COVID-19, $M_{before} = 3.66$, $SD_{before} = 1.50$, $M_{during} = 3.86$, $SD_{during} = 1.39$, $t(117) = 1.23$, $p = .220$ (Figure 6.1). On average, participants reported feeling "slightly socially connected" while engaging in digital social interactions both before and during COVID-19. However, feelings of connection derived from digital social interactions during COVID-19 were lower, relative to pre- COVID-19 levels, $M_{before} = 5.21$, $SD_{before} = 1.48$, $M_{during} = 4.87$, $SD_{during} = 1.57$, $t(117) = 2.75$, $p = .007$ (Figure 6.1). Participants reported using approximately three practices on average to participate in digital social interactions pre-pandemic, and this did not change after the onset of the pandemic, $M_{before} = 3.37$, $SD_{before} = 1.36$, $M_{during} = 3.33$, $SD_{during} = 1.58$, $t(117) = 0.30$, $p = .764$ (Figure 6.1). As shown in Figure 6.2, both before and after the onset of COVID-19, text messaging was by far the most popular primary practice for digital social interactions with friends, followed by video calling. There were no changes in the distribution of primary practice used for digital social interactions pre- to during- COVID-19 using a pairwise nominal symmetry test (Figure 6.2).

Objective in-person social isolation was quantified as household size. Participants reported an average household size of 2.43 ($SD = 1.38$) before the onset of COVID-19, and 2.90 ($SD = 1.48$) after the onset of COVID-19. This increase was not significant, $t(91) = 1.99$, $p = .050$, Bonferroni adjusted alpha = .008 (see Figure 6.3). However, household composition looked different after the onset of COVID-19 (using a pairwise nominal symmetry test) as many participants who reported living with roommate(s) before the pandemic reported living with family amid the pandemic, $p < .001$ (Figure 6.3). Participants reported that friends met their social needs "very well" before COVID-19 and "moderately" amid COVID-19, and this decrease was significant, $M_{before} = 4.21$, $SD_{before} = 0.86$, $M_{during} = 3.40$, $SD_{during} = 1.05$, $t(115) = 8.28$, $p < .001$, $d = 0.77$ (Figure 6.1). On average, participants reported "minimal" depressive symptoms before the onset of COVID-19 ($M = 8.12$, $SD = 8.72$), which significantly increased to "mild" after the onset of COVID-19 ($M = 16.47$, $SD = 10.66$), $t(118) = 12.00$, $p < .001$, $d = 1.10$ (Figure 6.1). On average, participants also reported that their happiness had decreased after the onset of COVID-19 (happiness change score), $M = -0.71$, $SD = 0.76$, $t(118) = 10.09$, $p < .001$, $d = 0.93$.

Figure 6.1 Pandemic Related Changes

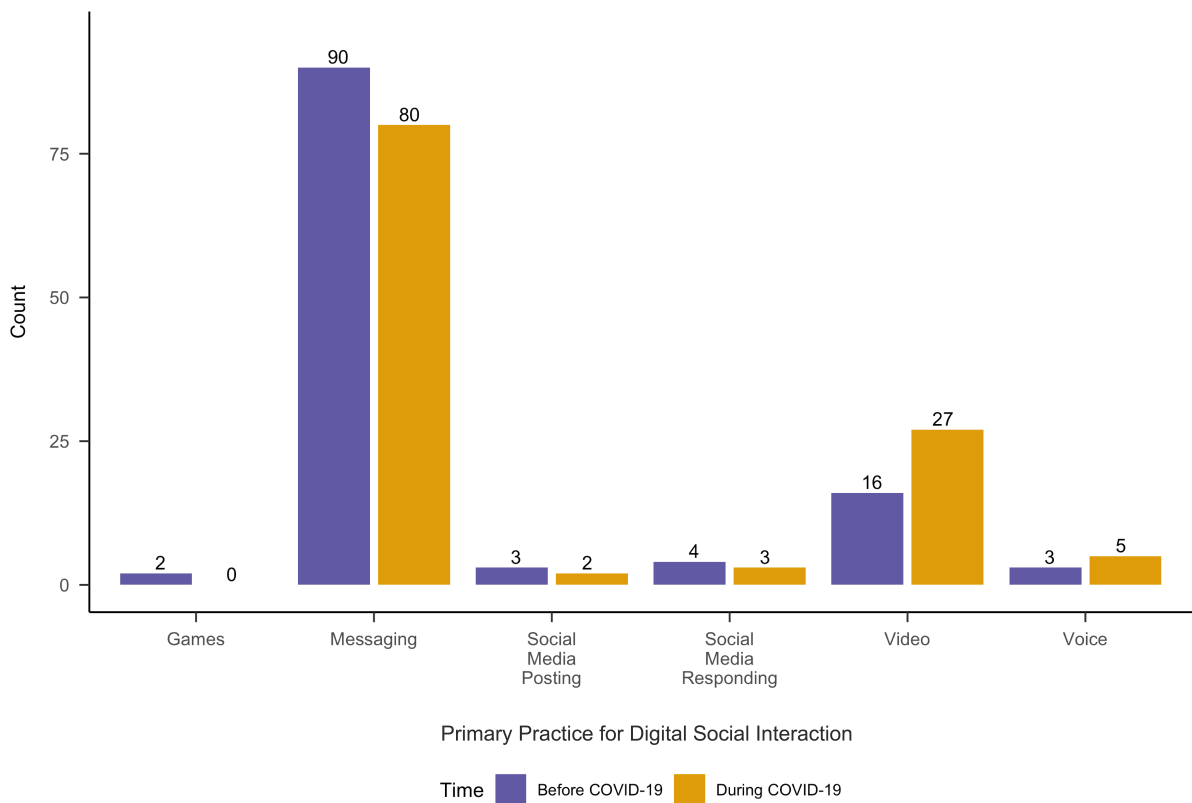


Note. Standardized z-scores for participants on several variables which were assessed currently (during COVID-19) and retrospectively (before COVID-19). Each dot represents an individual participant. The black diamonds represent the mean score of each set of observations and corresponding error bars. Individual dots are jittered horizontally for visibility. The mean comparisons which were significantly different during COVID-19 versus before COVID-19 are indicated with a bar and *, **, or ***. * Indicates a significant difference at the alpha corrected = .008 level. ** Indicates a significant difference at the alpha corrected = .002 level. *** Indicates a significant difference at the alpha corrected = .0002 level. *Source:* Reproduced from Towner, E., Tomova, L., Ladensack, D., Chu, K., & Callaghan, B. (2022b). *Current Research in Ecological and Social Psychology*. CC-BY 4.0.

6.3.2 Pre Pandemic Comparisons

Whether levels of loneliness, depression and happiness were different to past reports in similar samples collected before COVID-19 was explored. An independent samples *t*-test between loneliness levels in the present sample ($M = 41.07$; $SD = 14.85$) and in a comparable student sample ($M = 40.08$; $SD = 9.50$, $n = 487$; Russell 1996) revealed similar levels of loneliness, $t(604) = 0.69$, $p = .313$. Although the sample in this study did not exhibit significantly elevated average levels of loneliness relative to Russell (1996), this sample did exhibit significantly elevated average levels of depression, $M = 16.47$ ($SD = 10.66$) compared

Figure 6.2 Pandemic Related Changes in Primary Practice



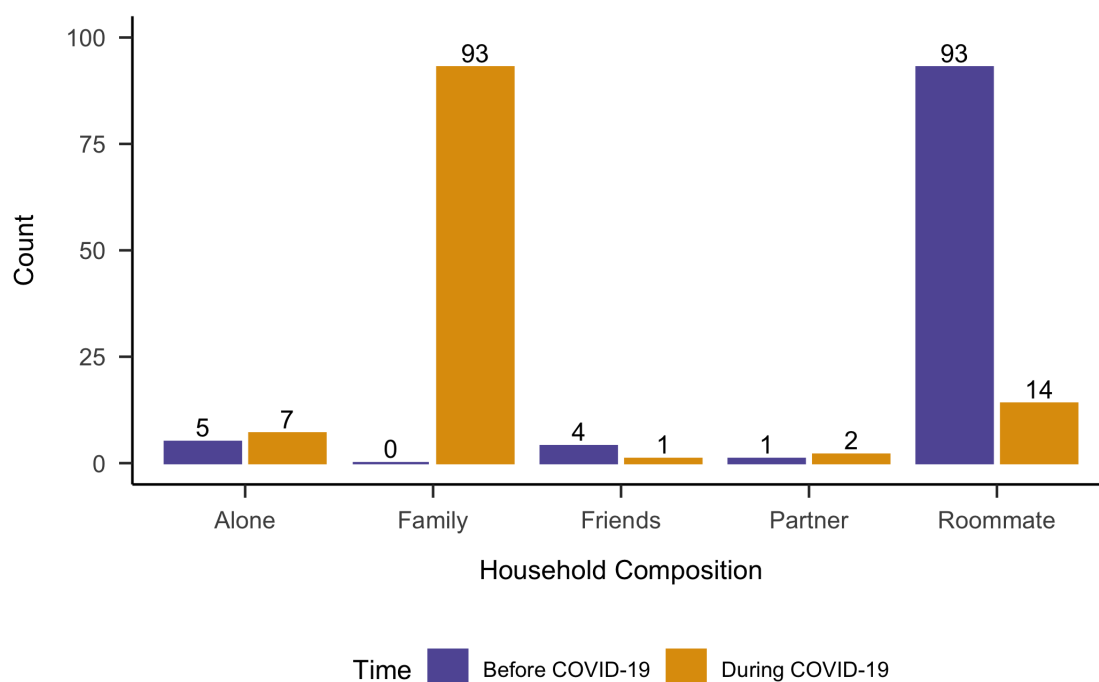
Note. The bars represent the number of participants who indicated each practice as their primary practice for digital social interaction with friends before COVID-19 and during COVID-19. Categories were mutually exclusive for each time point. One participant did not respond to the question, two participants indicated their prior but not current primary practice, and one participant indicated their current but not prior primary practice. *Source: Reproduced from Towner, E., Tomova, L., Ladensack, D., Chu, K., & Callaghan, B. (2022b). Current Research in Ecological and Social Psychology. CC-BY 4.0.*

to the Beck (1996) university student average, $M = 12.56$ ($SD = 9.93$, $n = 120$), $t(237) = 2.93$, $p = .006$. In addition, the sample in this study reported significantly lower levels of happiness ($M = 4.37$; $SD = 1.33$) than reported in university students from another study conducted prior to COVID-19 ($M = 4.89$; $SD = 1.11$, $n = 551$; Lyubomirsky and Lepper, 1999), $t(663) = 3.90$, $p < .001$.

6.3.3 Loneliness

Using multiple linear regression, how objective in-person social isolation (household size) and digital social interactions (frequency, number, connection and primary practice) were

Figure 6.3 Pandemic Related Changes in Household Composition



Note. The bars represent the number of participants with each household composition both prior to COVID-19 and during COVID-19. Categories were not mutually exclusive – for example participants might have lived with a partner and roommate and are therefore counted twice. *Source: Reproduced from Towner, E., Tomova, L., Ladensack, D., Chu, K., & Callaghan, B. (2022b). Current Research in Ecological and Social Psychology. CC-BY 4.0.*

associated with participants' ratings of loneliness amid COVID-19 was examined. There was a significant effect of objective in-person social isolation, whereby participants with a higher number of household members (less in-person social isolation) reported lower levels of loneliness during COVID-19, $b = -3.01$, $t(79) = 2.60$, $p = .011$, 95% CI = $[-5.32, -0.71]$. However, the effect of DSI frequency, DSI connection, DSI number of practices and DSI primary practice were not significant predictors of loneliness during COVID-19 in this sample, nor were there effects of age or sex on loneliness (see Table 6.1).

6.3.4 Depression

Using multiple linear regression, how objective in-person social isolation (household size) and digital social interactions (frequency, number, connection, and primary practice) were associated with participants' ratings of depression amid COVID-19 was examined. None of the

Table 6.1 Loneliness

	<i>b</i>	beta	<i>SE</i>	<i>t</i>	<i>p</i>
Intercept	46.12	0.00	26.76	1.72	.089
Age	0.11	0.01	1.27	0.09	.931
Sex	2.50	0.06	4.67	0.53	.594
Household Size	-3.01	-0.30	1.16	-2.60	.011*
DSI Frequency	2.32	0.22	1.36	1.71	.092
DSI Connection	-2.05	-0.20	1.16	-1.77	.080
DSI Number	0.68	0.07	1.15	0.60	.552
Primary Practice - Social Media Posting	8.23	0.08	11.15	0.74	.463
Primary Practice - Social Media Responding	-0.84	-0.01	8.89	-0.09	.925
Primary Practice - Video Calling	7.43	0.21	4.29	1.73	.087
Primary Practice - Voice Calling	-9.80	-0.10	10.51	-0.93	.354

Note. DSI primary practice is compared to "Messaging" as the reference group. * indicates significance at the alpha corrected = .017 level. ** indicates significance at the alpha corrected = .003 level. *** indicates significance at the alpha corrected = .0003 level. *Source:* Reproduced from Towner, E., Tomova, L., Ladensack, D., Chu, K., & Callaghan, B. (2022b). *Current Research in Ecological and Social Psychology*. CC-BY 4.0.

variables were significantly associated with depression during COVID-19 when correcting for multiple comparisons (see Table 6.2).

6.3.5 Happiness

Using multiple linear regression, how objective in-person social isolation (household size) and digital social interactions (frequency, number, connection, and primary practice) were associated with participants' ratings of current happiness during COVID-19 was examined. There was a significant effect of household size, whereby participants with a higher number of household members reported higher levels of happiness, $b = 22.86$, $t(75) = 3.30$, $p = .001$, 95% CI = [9.06, 36.65]. None of the other variables were significantly associated with current happiness during COVID-19 when correcting for multiple comparisons (see Table 6.3).

6.4 Discussion

Overall, and in line with prior research, evidence suggested that emerging adults suffered reduced mental health and changes in social support during the pandemic (Halliburton et al., 2021; Kujawa et al., 2020; Minhas et al., 2021). In these analyses, there was a large increase in depression, a large decrease in happiness and a large decrease in participant ratings of their

Table 6.2 Depression

	<i>b</i>	beta	<i>SE</i>	<i>t</i>	<i>p</i>
Intercept	2.86	0.00	17.99	0.16	.874
Age	0.70	0.09	0.85	0.83	.411
Sex	-2.29	-0.08	3.14	-0.73	.469
Household Size	-1.76	-0.25	0.78	-2.26	.027
DSI Frequency	1.64	0.22	0.91	1.79	.077
DSI Connection	-1.40	-0.20	0.78	-1.80	.075
DSI Number	1.82	0.27	0.77	2.36	.021
Primary Practice - Social Media Posting	7.55	0.11	7.50	1.01	.317
Primary Practice - Social Media Responding	5.57	0.10	5.98	0.93	.354
Primary Practice - Video Calling	1.81	0.07	2.89	0.63	.533
Primary Practice - Voice Calling	-5.67	-0.08	7.07	-0.80	.425

Note. DSI primary practice is compared to "Messaging" as the reference group. * indicates significance at the alpha corrected = .017 level. ** indicates significance at the alpha corrected = .003 level. *** indicates significance at the alpha corrected = .0003 level. *Source:* Reproduced from Towner, E., Tomova, L., Ladensack, D., Chu, K., & Callaghan, B. (2022b). *Current Research in Ecological and Social Psychology*. CC-BY 4.0.

Table 6.3 Happiness

	<i>b</i>	beta	<i>SE</i>	<i>t</i>	<i>p</i>
Intercept	247.56	0.00	166.01	1.49	.140
Age	-6.02	-0.08	7.86	-0.77	.446
Sex	-14.46	-0.06	27.19	-0.53	.597
Household Size	22.86	0.38	6.93	3.30	.001**
DSI Frequency	-9.27	-0.15	8.17	-1.13	.260
DSI Connection	14.66	0.25	7.04	2.08	.041
DSI Number	-2.21	-0.04	6.86	-0.32	.748
Primary Practice - Social Media Posting	-61.97	-0.11	64.80	-0.96	.342
Primary Practice - Social Media Responding	3.84	0.01	60.31	0.06	.949
Primary Practice - Video Calling	-29.36	-0.14	26.05	-1.13	.263
Primary Practice - Voice Calling	71.66	0.13	60.87	1.18	.243

Note. DSI primary practice is compared to "Messaging" as the reference group. * indicates significance at the alpha corrected = .017 level. ** indicates significance at the alpha corrected = .003 level. *** indicates significance at the alpha corrected = .0003 level. *Source:* Reproduced from Towner, E., Tomova, L., Ladensack, D., Chu, K., & Callaghan, B. (2022b). *Current Research in Ecological and Social Psychology*. CC-BY 4.0.

social needs being met by peers, post-pandemic onset. Participants also rated their depression as more severe and their happiness as lower than in similar samples collected before the onset of the pandemic. Moreover, feelings of connection from digital social interactions decreased. The hypothesis that frequency of digital social interactions would be negatively associated with loneliness was not supported. Contrary to expectations, there was no association in the data between DSI frequency and loneliness, suggesting that use patterns were not associated with feelings of loneliness. However, there was an association between objective in-person social isolation and loneliness. Although household size did not change on average across the sample from pre- to post- pandemic onset, those with larger household sizes were less lonely (and were also happier) than those with smaller household sizes amid the pandemic. As over 68% of the sample did not ordinarily live with family but returned home to live with family during the virus outbreak, it is possible that greater household size might have been a proxy for familial support during COVID-19, demonstrating a potential "protective effect" of family for the emerging adults in this study. Similarly, another study found that maternal support in particular was helpful for emerging adults' psychological health (van den Berg et al., 2021).

Surprisingly, self-reported loneliness in this sample was not elevated compared to demographically similar samples from before the COVID-19 pandemic. This result, coupled with the fact that the hypothesised relationship between digital social interactions and loneliness in this sample was not observed is notable. In fact, the direction of the association between digital social interactions and loneliness (although not significant) was in the opposite than expected direction; that is, more frequent digital social interactions were associated with higher loneliness scores. It is possible that because emerging adults generally, and university students specifically, were already a high loneliness population before the pandemic (Hammond et al., 2019), a ceiling effect was operating in this study in the ability to detect increased loneliness. However, it is also possible that these results support the findings from the empirical study of social isolation presented in Chapters 2–3. While digital interactions might be effective in remediating feelings of loneliness, they might not be sufficient to ward off negative consequences, such as the potential negative impact of isolation on mental health. However, due to the observational nature of this study, it is possible that those who were less lonely (perhaps due to increased household size) sought out DSI less frequently. Therefore, the influence of DSI on loneliness may depend on one's level of in-person social contact.

It is important to also consider the ways that mental health influences the usage (and, thus, the potential effectiveness) of DSI. Individuals who are happy may derive more feelings of connection from DSI and they may use DSI in ways that promote and facilitate social connection. For example, Ping et al. 2020 found that happier individuals used DSI to share information or enhance friendships. Conversely, individuals with lower levels of happiness more often

used DSI for entertainment or to avoid loneliness (Holmberg, 2014). Research also supports the idea that DSI can be used in connection-promoting ways (e.g., self-disclosure promoting intimacy and relational closeness; Ledbetter et al., 2011) and non-connection promoting ways (e.g., passive viewing, and social comparison; Clark et al., 2018; Valkenburg et al., 2021). Thus, increasing the quantity of DSI may enhance wellbeing only if the quality of social connection is concurrently increased.

Importantly, in this study, only spontaneous usage patterns of DSI was examined, and the vast majority of participants indicated that messaging/texting was their primary mode of digital social interaction with friends both before and after the onset of COVID-19. While messaging/texting can be connection-promoting, Kumar and Epley (2021) showed that interactions including voice created stronger social bonds compared to interactions including only text. It is possible that directed DSI interventions might be more effective in promoting wellbeing than spontaneous DSI usage. Indeed, a recent study investigated an intervention which created digital "small groups" for social interactions among seniors during COVID-19 (Shapira et al., 2021) and results indicated that these directed digital social interactions resulted in reduced loneliness and depression.

In this study, objective in-person social isolation was associated with lower happiness and higher loneliness, yet there was no association between digital social interactions and loneliness, depression or happiness. Much research has been conducted in recent years on digital communication technologies and their impacts (both positive and negative) on mental health (Ellison et al., 2007; Hall et al., 2021; Hsu et al., 2011; Lou et al., 2012; Parks and Roberts, 1998; Shaw and Gant, 2002; Verduyn et al., 2017; Whitty, 2008). However, although emerging adults spend much time utilising digital communication methods, they also typically experience a rich and varied social landscape in-person. While past research has suggested that social media can be beneficial for social interactions (Pew Research Center, 2018), the COVID-19 crisis allowed the investigation of digital social interactions at a time of drastically reduced in-person social interactions.

Chapter 7

The Fear of Missing Out during COVID-19

7.1 Introduction

Findings from the previous chapter (Chapter 6) indicated a reduction in mental health and changes in social support among emerging adults during the COVID-19 pandemic. The analyses, however, did not yield support for the hypothesised buffering effect of digital social interactions against social disconnection. To broaden this investigation, the current chapter utilised a qualitative and mixed-methods approach to explore the emotional experiences of young people during this unprecedented period of social disconnection. The COVID-19 pandemic fundamentally disrupted daily life worldwide, with a particular impact on young people at critical developmental stages. Beyond its devastating public health toll and over seven million deaths, the pandemic's containment measures – including lockdowns, social distancing, and institutional closures – reshaped how people lived, worked and connected with others (Rohrich et al., 2020). The media has dubbed young people who grew up during the pandemic the "COVID Generation" (Fawcett, 2022; Hill, 2022; Lesonsky, 2024). In the pandemic's aftermath, studies have found longitudinal increases in childhood depressive symptoms (Bignardi et al., 2021), increased suicide rates among children and adolescents (Tanaka and Okamoto, 2021) and mental health challenges in more than a third of high school students (Rico et al., 2022).

As mentioned in the previous chapter (Section 6.1) emerging adulthood is a stage of adolescence spanning from the late teens through the twenties (Arnett, 2011, 2024). During this period, individuals often move away from home but are not yet fully settled in adult roles. This phase continues to evolve today as young people pursue higher education for longer durations, face prolonged job instability, and delay marriage and parenthood compared to prior generations (particularly in the Global North; Settersten and Ray 2010). COVID-related disruptions were especially significant for emerging adults for several reasons. Emerging adulthood has

been characterised by five key features: identity exploration, instability, self-focus, feeling in-between, and unparalleled opportunities for life transformation (Arnett, 2024). The pandemic directly threatened each of these developmental hallmarks – by restricting exploration, amplifying instability, forcing focus on collective rather than individual needs, prolonging the "in-between" state, and dramatically limiting opportunities. Emerging adulthood also involves experiences highly susceptible to pandemic disruption, such as attending university, moving into shared housing, travelling abroad, or undertaking internships. Finally, while this life stage usually offers flexibility and freedom, it is also marked by heightened anxiety and uncertainty (Iannattone et al., 2024), which the pandemic likely exacerbated (Glowacz and Schmits, 2020).

Studies have confirmed that emerging adults' mental health was disproportionately affected by the pandemic (Pierce et al., 2020). This age group reported particularly high levels of psychological distress (Gramlich, 2023), with two-thirds experiencing moderate to severe anxiety and depression symptoms and one-third reporting suicidality (Halliburton et al., 2021). Longitudinal research directly comparing COVID-related stressors between young adults and adolescents found greater impacts in young adults (Villanti et al., 2022). While average trends showed declining life satisfaction and mental health among young adults amid the pandemic, individual responses varied considerably (Preetz et al., 2021). Protective factors included social integration and having an intimate partner, while risk factors included limited peer contacts and returning to the parental home – experiences that directly relate to the developmental goals of emerging adulthood (Preetz et al., 2021).

Understanding why emerging adults were vulnerable to pandemic-related mental health challenges is crucial for both theoretical and practical reasons. Theoretically, it can illuminate how stressful environmental events can disrupt developmental processes and subsequently affect wellbeing. Practically, this knowledge is essential for designing interventions to support emerging adults through both ongoing long-term pandemic impacts and future societal disruptions. Further, mixed-methods research can help explore how young adults viewed and made meaning of the COVID-19 pandemic – an important consideration given that personal narratives and meaning-making processes have been shown to have significant mental health implications (Adler et al., 2013). Using the theoretical framework underlying developmental goals during this period might help clarify these mental health impacts.

7.1.1 The Current Study

Using a mixed-methods approach, the current study examined two key questions: (Q1) What were the emotional experiences of emerging adults during the immediate onset of the pandemic?; and (Q2) How did these emotional experiences relate to changes in mental health for emerging adults? Combining qualitative analysis of personal narratives with quantitative

mental health measures allowed a nuanced investigation of pandemic experiences and mental health challenges among emerging adults during COVID-19.

7.2 Methods

This chapter is a part of the COVID study described in the previous chapter (Chapter 6). Therefore, the participants, procedures and study design in this chapter are identical to those described in the previous chapter with one exception: given the qualitative and mixed-methods nature of this investigation, all ($n = 126$) participants were included in these analyses (rather than participants aged 26 – 29 years being excluded as in the previous chapter). For this set of analyses, the qualitative written responses and a subset of the larger survey's questionnaires were examined.

7.2.1 Measures

7.2.1.1 Qualitative Measure

Written Reflection. The primary measure analysed in this study was a qualitative long-form written response regarding the impact of the COVID-19 pandemic. The question, adapted from Pennebaker (1997), asked participants to "write about (their) very deepest thoughts and feelings about the way COVID-19 has affected (them) and (their) life for five consecutive minutes without stopping".

7.2.1.2 Quantitative Measures

Change in Depressive Symptoms. As reported in Chapter 6, the Beck Depression Inventory-II (BDI-II) was used to measure depressive symptomatology (Beck et al., 1996). Participants were asked to report how they felt in the last two-week period (i.e., during COVID-19) as well as retrospectively for a typical two-week period before the onset of COVID-19. A change score was calculated by subtracting the "retrospective" score from the "current" score. Therefore, a higher change score indicates worsened depressive symptomatology.

Change in General Mental Health. Participants were asked to indicate more generally whether they felt their mental health had changed after the onset of the COVID-19 pandemic. Participants rated changes in their mental health since the onset of COVID-19 using a 5-point scale (1 = "much worse" to 5 = "much better"). Responses were recoded (-2 = "much better"

to 2 = "much worse"). Therefore, positive scores indicated worsened mental health, negative scores indicated improved mental health and zero indicated no change.

Covariates.

Subjective Social Status. Subjective social status was measured using the MacArthur Scale of Subjective Social Status (Adler et al., 2000). This scale measures an individual's perception of their own place within the social hierarchy. Participants are instructed to picture a ladder and indicate where they stand relative to others, with the top rung representing the highest status. Rungs range from 1 (lowest social status) to 10 (highest social status).

7.2.2 Data Analysis

7.2.2.1 Emotional Experiences

Qualitative responses were coded in NVivo (Lumivero, 2017). Categories were not pre-defined but crafted based on frequency among responses (Khandkar, 2009). A bottom-up inductive approach was used with some theoretical expectations based on previous research about the negative impact of COVID-19 on mental health on populations broadly and young adults in particular (Brooks et al., 2020; Holmes et al., 2020; Pfefferbaum and North, 2020). First, two coders (CS and KC) read the written responses and looked for initial patterns in the data. The coders independently took notes and developed category lists based on common topics that emerged. Through discussion, major themes were defined and a codebook was established (See Table 7.1). The data were then reanalysed by the primary coder (CS) using the agreed upon codebook to determine frequency counts of themes within the data. The theme categories were not considered mutually exclusive; therefore, participant responses could be coded as endorsing more than one theme. If the primary coder was unsure how to code a portion of the data based on the information in the codebook, they consulted the secondary coder (KC), and through discussion, agreed jointly on the appropriate code(s) for that section of text.

The data coders brought relevant experiential and academic perspectives to the qualitative analysis. The primary coder (CS) was a research assistant with interests in social relationships and mental health. As someone who was 24 years old when the pandemic began, CS experienced the COVID-19 pandemic as an emerging adult herself, providing insider perspective on the developmental challenges faced by this age group. The secondary coder (KC) was the lab manager with expertise in emotion regulation, anxiety and depression across the lifespan. At 23 years old during the pandemic onset, KC also had lived experience as an emerging adult

during this period. Both coders' positions as emerging adults during the pandemic provided valuable phenomenological insight into participants' experiences, while their research training informed their analytical approach. To maintain rigorous analysis, the coders acknowledged their shared generational perspective could potentially influence interpretation. They addressed this through systematic use of the codebook, independent initial coding, regular discussion to resolve discrepancies and grounding all interpretations directly in participants' written responses.

7.2.2.2 Emotional Experiences and Changes in Mental Health

First, overall self-reported changes in mental health after the onset of the COVID-19 pandemic were characterised by conducting one-sample *t*-tests on the mental health variables of interest (change in depressive symptoms and change in general mental health (results regarding changes in depressive symptoms were previously reported; Towner et al., 2022b).

Mixed-methods analyses were used to examine how themes participants discussed in their written responses mapped onto these quantitative mental health variables of interest. To do this, two general linear regressions were conducted. Change in depressive symptoms and change in general mental health were entered into the models as the two outcomes of interest. As predictors, each theme (dummy coded for whether or not each participant described that theme) was entered into the model. Sex/gender, age and subjective social status were also entered into the model as covariates. For both sets of analyses the Bonferroni method for multiple comparisons was used to determine statistical significance (two outcomes – change in depressive symptoms and change in general mental health) for an adjusted alpha level of .025 (.05/2).

Table 7.1 Thematic Codebook – COVID-19 Experiences

Theme	Definition
Lost Opportunities	Sentiments shared by participants about having access to various opportunities taken away due to COVID-19 quarantine restrictions or cancellations. Examples included: graduation ceremonies, internships, jobs, study abroad, vacations with family or friends, funerals, birthdays, etc.

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Theme	Definition
Gained Opportunities	Sentiments shared by participants about opportunities that they had gained because of the additional time and distance in their lives due to the COVID-19 pandemic. Examples included more time spent with family at home, more phone calls with long-distance friends, virtual game nights, self-care activities, exercise routines, time to study, time to prepare for their career goals, etc.
Loneliness	Feelings shared by participants about being isolated from other people and wishing that they had more social support through the COVID-19 pandemic. This includes friendships that dissipated from the newfound geographic distance between them and disruptions with their daily routines. Other examples include feeling lonely in romantic relationships that became long-distance or ended because of the COVID-19 pandemic, as well as loneliness felt by being surrounded by family members that they did not connect with due to requirements to leave their current housing.
Social Support	Statements shared by participants about feelings of being social supported throughout the COVID-19 pandemic. Social support and loneliness are not mutually exclusive themes. Social support included gaining new digital friends, reconnecting with old friends remotely, spending more time with family in ways that felt supportive, and having close friends in their 'pod' that they could spend quality time with in-person.

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Theme	Definition
Gratitude	This theme includes mentioning of joyful moments throughout the COVID-19 pandemic that participants felt lucky to have in their life. These include their health [not having COVID], being surrounded by loved ones, the capacity to work remotely compared to essential or frontline workers, the ability to transition their friendships to online platforms, leniency from academic professors on grading given the circumstances, and time to focus on themselves given constraints to interacting with others.
Negative Thoughts	Negative thoughts encompassed ruminating thoughts about their emotional state, their self-worth, or about the state of society. Examples include fixating on frustrations about their current state of living, thoughts that this is how the world will now function indefinitely, and negative statements about their health and well-being.
Self-Reflection	Self-reflection was defined as statements shared by participants about having additional time to self-reflect and journal during the lockdowns. This includes being introspective about their peer and romantic relationships, career goals, gender and sexual identities, and self-care and/or health-related aspirations.

Note. Definitions of key themes identified in participants' written responses about their experiences during the COVID-19 pandemic. Themes include Lost Opportunities, Gained Opportunities, Loneliness, Social Support, Gratitude, Negative Thoughts and Self-Reflection.

7.3 Results

7.3.1 Emotional Experiences

There were 126 participants who completed the qualitative response question. For each emergent theme (including "lost opportunities", "gained opportunities", "loneliness", "social support", "gratitude", "negative thoughts" and "self-reflection") examples, sample quotations and frequency counts are provided below.

7.3.1.1 Lost Opportunities

Most respondents ($n = 75$) made statements about a change in their life that they perceived as a loss or negative consequence of the COVID-19 pandemic. Some of these "lost opportunities" included participation in certain ceremonies (e.g., graduation, community gatherings, funerals), cancelled travel (e.g., family vacations, trips with peers, study abroad opportunities), and career advancing opportunities such as internships and networking events.

For example, one said:

As a pre-med student, I have become extremely fearful of the future in regards to internship, research, job, MCAT, and so forth. I had really wanted this academic quarter to be a quarter where I can achieve a lot for my future, but COVID-19 has halted so much of these plans. Right now, I feel like I can just do well in classes (or as well as I can at the moment) and not continue extracurriculars and strengthen other aspects for med school.

Another person more broadly mentioned barriers to feeling accomplished:

I feel like I've wasted three years at (undergrad university) and I want to find some way to accomplish something before I graduate. With the pandemic, I feel there is even less time for me to do something meaningful.

Another person discussed a cancelled educational opportunity:

This virus took away one of the four years that I could compete in a (organisation name) national championship for my dream school. I was having the season of my life as I was exceeding my expectations of what my first athletic season in college would have been. I couldn't wait to compete at a national championship my freshman year.

7.3.1.2 Gained Opportunities

Many participants ($n = 42$) described how they benefited in some way from a change in their life due to the COVID-19 pandemic. The most often mentioned "benefit" of the pandemic was more time to dedicate to their social network and personal goals. More specifically, people mentioned the increased capacity for self-care practices, as one person said:

I have taken the opportunity of being at home more often to eat healthier, exercise, sleep more, and concentrate on my studies, as a way to come out of this pandemic with some positives and keep my mental health in check.

Other people discussed the normalisation of remote interactions during the pandemic which reconnected them to old friends:

It has also increased my connectedness with old friends, who I would normally talk to sporadically. We now have weekly zoom calls to catch up, which is more than this group of friends has talked all together in years.

7.3.1.3 Loneliness

Many participants ($n = 38$) expressed feeling socially isolated at some point during the COVID-19 pandemic. This category encompasses feelings of isolation due to social distancing mandates, relocating to family homes away from normal social networks, and challenges navigating romantic relationships.

One person expressed:

Feeling lonely has probably been the number one issue I have been experiencing with COVID.

Other respondents shared feeling discouraged about their social life generally as well as their dating prospects:

I crave social interaction since I am not talking to people as much, I try to call at least one friend every day but that is still much fewer than the amount of people I would hang out with in a day at (university name). It's also much easier to meet people on campus, and I miss doing that as well. In terms of romantic partners, I am single and have been for a long time but at school enjoyed meeting new people, and I use a dating app now, but it feels like there's no point because I can't meet up with these people in person.

7.3.1.4 Gratitude

Many respondents ($n = 35$) expressed gratitude in their written responses. Some of the things that participants were grateful for included the leniency shown to them by professors in the deadlines for their work, the ability to spend more time with family and friends, the time and space to dedicate to taking care of themselves, their health (i.e., not being immunocompromised, not contracting COVID-19), their jobs (e.g., the ability to work remotely), appreciation for frontline workers, and gratitude for moments in their life that they took for granted before the pandemic.

For example, one person explained:

Everyone is so caught up with themselves and we often take the little things for granted. Although it is very scary, I have been able to spend more time with my son and my mother.

Similarly, another person mentioned:

I am more mindful and appreciative of life in general and the fact that I am currently healthy with no signs of the virus. I am grateful for this time where I can slow down and absorb this calmer period before everything starts back up.

7.3.1.5 Social Support

Some participants ($n = 18$) expressed feeling socially supported during the COVID-19 pandemic, particularly by family members. Examples of social support included spending time with family, being reconnected with friends either by relocating geographically or increased remote contact, and more quality time spent with significant others.

One person mentioned that the pandemic allowed her to see her friends, family, and boyfriend in person more:

All of my close friends came home, and my mom is really happy about me being home. . . My boyfriend, whom I did long distance with during college (no serious issues with long distance fortunately) is also home now and I see him much more often than I would if the pandemic never happened. . . Seeing my friends is a great plus to this whole thing, as well as spending time with my family.

Another person shared:

Because I have been home for longer now than I have in years, I feel much more connected to my family and feel like I can reach out to them more in my times of need.

7.3.1.6 Negative Thoughts

Some participants ($n = 13$) expressed having thoughts that they described as negative, intrusive, or self-critical. Participants expressed frustrations about societal responses to the pandemic, feeling limited hope for the future, feeling agitated for being ‘stuck’ at home, and having negative thoughts about their self-worth.

One person highlighted the emotional toll of financial challenges their family experienced:

Both my parents have to be on unemployment, and we cannot buy the things we used to. Everyone is rationing their money. I feel really low, and depressed, and discouraged about the future and I know many of my friends and peers feel the same. I am starting to think that the mental impact this is going to have on people, is worse than the virus itself.

Another person talked about negative rumination more generally.

I just really feel like COVID-19 has allowed for people to explore/reopen past traumas. I think about how I'm not done grieving the loss of my father that happened almost 2 years ago, I get worried about my mother's and brother's health and our financial situation. What bothers me the MOST though is how my mind just goes to really dark, unwanted, and disturbing places. It makes me feel ashamed for thinking such horrible things.

7.3.1.7 Self-Reflection

Some participants ($n = 8$) expressed how the COVID-19 pandemic prompted them to self-reflect in a way they described as positive and helpful. This type of self-reflection applied to career goals, relationships (e.g., family, peer, romantic), identity, and values.

For example:

The pandemic has allowed time for me to reflect on what I want to do post-graduation and set goals for myself to aspire to.

One participant shared what they learned about their sexual identity:

One good thing about quarantine is that it has given me a lot of time to self-reflect, and this has led to me making a lot of self-realizations. The most important of which is realising that I am a lesbian. I knew that I liked girls, and I knew that I didn't feel the same about men, but it took weeks of being alone with my thoughts for me to process and accept that. Now I'm very excited that I'm finally being myself!

7.3.2 Emotional Experiences and Changes in Mental Health

As reported in Chapter 6, on average, participants reported that their depressive symptoms had increased by 8.33 points relative to prior to the pandemic (95% CI = [7.01, 9.64], $SD = 7.45$, Min = -9, Max = 33), $t(125) = 12.54$, $p < .001$, $d = 1.17$). Participants also reported that,

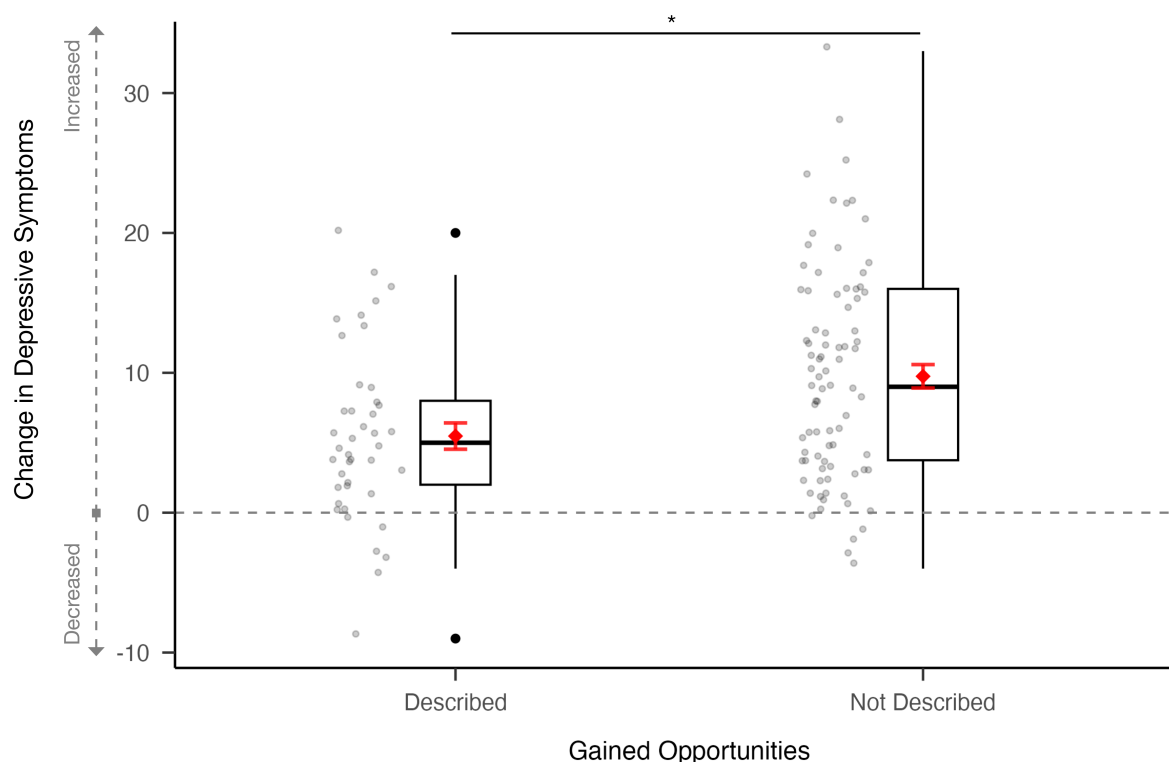
on average, their general mental health worsened relative to prior to the pandemic ($M = 0.43$, 95% CI = [0.30, 0.56], $SD = 0.75$, Min = -1 , Max = 2), $t(125) = 6.39$, $p < .001$, $d = 0.57$).

Participants who described gained opportunities in the content of their emotional reflection reported smaller increases in depressive symptoms post-pandemic onset compared to participants who did not describe gained opportunities (Estimate = -4.93 , Standardised Estimate = -0.31 , $SE = 1.44$, $p < .001$), controlling for the expression of all other themes (lost opportunities, loneliness, social support, gratitude, negative thoughts, and self-reflection) as well as sex, age and subjective social status (Figure 7.1). Similarly, controlling for the expression of all other themes as well as sex, age and subjective social status, participants who described gained opportunities in the content of their emotional reflection reported less worsening of their general mental health post-pandemic onset compared to participants who did not describe gained opportunities (Estimate = -0.44 , Standardised Estimate = -0.27 , $SE = 0.15$, $p = .004$) (Figure 7.2). Further, controlling for the expression of all themes in the content of the emotional reflection as well as sex and age, those who reported higher subjective social status reported smaller increases in depressive symptoms post-pandemic onset (Estimate = -0.87 , Standardised Estimate = -0.20 , $SE = 0.38$, $p = .022$).

7.4 Discussion

In this chapter, the emotional experiences of emerging adults after the immediate onset of the COVID-19 pandemic as well as how these emotional experiences were associated with pandemic-related changes in mental health were investigated. As reported in Chapter 6, participants indicated that their mental health largely worsened after the onset of the COVID-19 pandemic. In line with other studies, participants expressed feelings related to social support, social isolation and loneliness (McKinlay et al., 2022; Shanahan et al., 2023; Vaterlaus et al., 2021), gratitude (Di Blasi et al., 2024), negative thoughts (Hager et al., 2022; Halder and Samajdar, 2022) and self-reflection (Crăciun, 2024). However, the most prominent themes that emerged from the qualitative data had to do with changes in available and accessible opportunities for achievement. Approximately 60% of participants (75/126) described lost opportunities in some way during their emotional reflection. Further, these reflections suggested that several key features that distinguish emerging adulthood from other stages of life were particularly disrupted or exaggerated by the COVID-19 pandemic. For example, the ability to try out different ways of living or different options for love and work was severely curtailed by social distancing restrictions that put a halt to major social events and in-person work and learning experiences. The sample in this study largely consisted of university students and many participants had to unexpectedly leave university and return to their family homes (as

Figure 7.1 Depressive Symptoms and Gained Opportunities

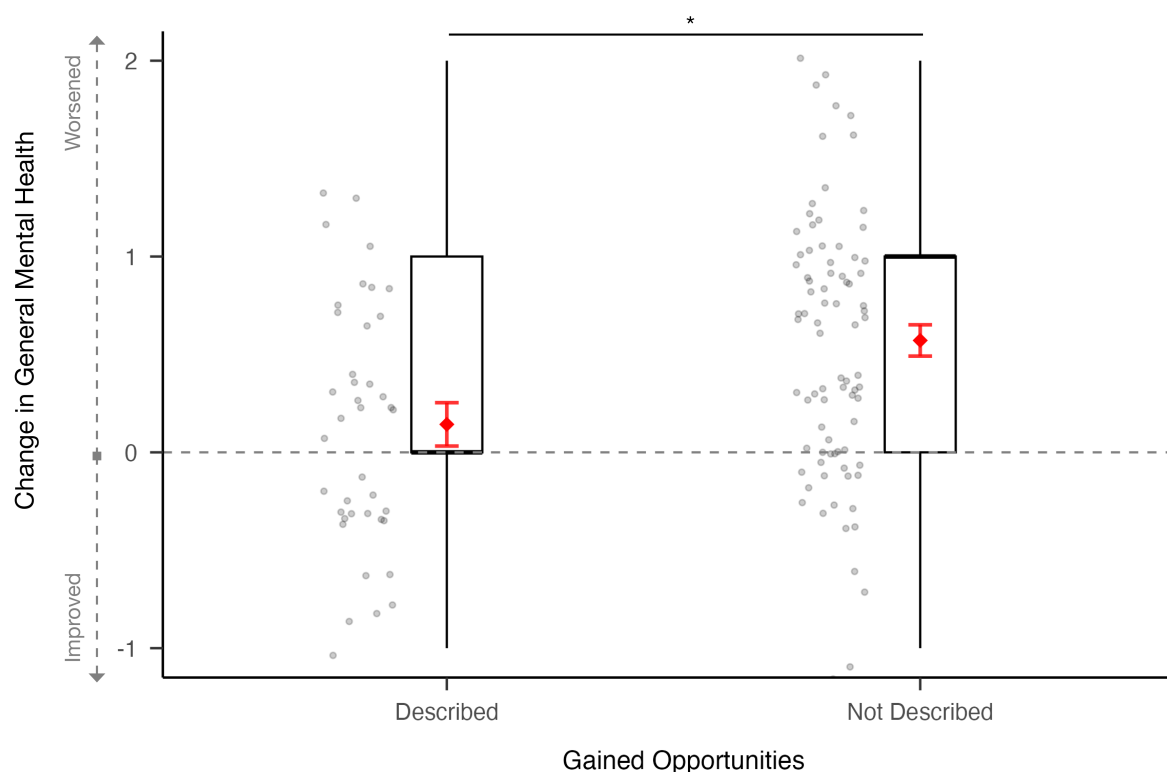


Note. This figure represents the change in depressive symptoms after the onset of the COVID-19 pandemic stratified by whether participants expressed themes of "gained opportunities" in the written emotional reflection. The grey dots represent each participant's depressive symptom change score. Boxplots show the sample median and interquartile range (outliers are represented by black dots). Red diamonds represent the sample mean (and error bars). Scores above zero indicate an increase in depressive symptoms post pandemic onset, scores below zero indicate a decrease in depressive symptoms post pandemic onset and a score of zero represents no change. The star represents a significant difference between the two group means at the Bonferroni adjusted alpha level of .025.

reported in Chapter 6) – experiencing less autonomy over their decisions and choices. This shift likely resulted in fewer opportunities for self-focus. Further, uncertainty around the end of the virus and restrictions likely heightened the instability that already characterises this period. Finally, the sense of endless possibilities and optimism that is typical of emerging adults might have been dampened by the harsh realities of the pandemic – including illness, death, and financial hardships as reflected by the negative thoughts included in some participants' written responses.

Overall, these results support and add to the literature which has identified "opportunities" as a key source of concern among emerging adults in the immediate aftermath of the pandemic

Figure 7.2 Mental Health and Gained Opportunities



Note. This figure represents the change in general mental health after the onset of the COVID-19 pandemic stratified by whether participants expressed themes of "gained opportunities" in the written emotional reflection. The grey dots represent each participant's mental health change score. Boxplots show the sample median and interquartile range (outliers are represented by black dots). Red diamonds represent the sample mean (and error bars). Scores above zero indicate a worsening in general mental health post pandemic onset, scores below zero indicate an improvement of general mental health post pandemic onset and a score of zero represents no change. The star represents a significant difference between the two group means at the Bonferroni adjusted alpha level of .025.

onset (McKinlay et al., 2022; Shanahan et al., 2023). These findings support the idea that the pandemic challenged emerging adults' abilities to achieve relevant developmental goals such as moving out of the family home, gaining autonomy, developing a professional identity, and exploring romantic relationships (Arnett, 2000; Crăciun, 2024; Rauer et al., 2013; Taylor et al., 2013). Further, these results extend previous findings by mapping qualitative emotional experiences on to quantitative measures of mental health (Dotson et al., 2022). While approximately 41% (52/126) of participants described only lost opportunities, 18% (23/126) described both lost and gained opportunities. Importantly, those who described gained opportunities (whether

or not they also described lost opportunities) reported smaller increases in depressive symptoms post-pandemic onset and less worsening of their general mental health.

Beyond "gained opportunities" participants also expressed additional positive aspects of their experience of the pandemic. Nearly 30% of participants expressed gratitude—for their health and ability to work remotely—while others highlighted positive aspects such as enhanced social support through digital reconnection with friends, increased time with family and opportunities for self-reflection like setting goals and making personal realisations. These positive reflections underscore the diverse experiences of this study's participants and showcase their resilience during this challenging time. However, it is important to note that positive reflections might also reflect diversity in lived experiences amid the pandemic. The severity of challenges faced likely varied considerably based on individuals' socioeconomic circumstances and available resources. Participants who described gained opportunities might have experienced more favourable circumstances, rather than simply maintaining an optimistic perspective. Consistent with this idea and existing literature (Rodriguez-Stanley et al., 2024), these findings reveal that participants with higher subjective social status experienced smaller increases in depressive symptoms following the onset of the pandemic. This association persisted even when accounting for participants' qualitative expressions of gained opportunities. However, subjective social status might not fully encapsulate the actual changes in opportunities encountered by participants. Additionally, it is challenging to distinctly separate the intertwined dynamics among available opportunities, social status and mental health. Although these results indicate a positive relationship between the expression of gained opportunities and improved well-being—even when controlling for subjective social status—caution should be exercised against assuming that promoting a "positive mindset" alone is sufficient to mitigate the mental health challenges during the pandemic. Instead, these findings highlight the importance of fostering both tangible and perceived opportunities for emerging adults during challenging times.

This chapter explored the experiences of emerging adults at the onset of the COVID-19 pandemic. Findings demonstrate that participants experienced challenges related to core features of their developmental stage, particularly regarding academic and career opportunities. Importantly, those who identified gained opportunities despite the pandemic's constraints reported less detrimental mental health impacts, suggesting a critical role for fostering developmental goals even amid life disruptions. The distinctive nature of this crisis merits special consideration. Unlike other collective traumas that often unite communities, COVID-19 necessitated physical separation and "staying-at-home" precisely when emerging adults were seeking independence and exploration. Paradoxically, those at low physical risk from the virus – adolescents and young adults – were asked to make substantial sacrifices that worked against their developmen-

tal needs. This unique contradiction is interesting given the particularly strong mental health impacts observed in this population.

These results highlight the importance of recognising emerging adulthood (and late adolescence) as an important developmental period with specific needs and vulnerabilities. While younger adolescents likely continued to live in their usual home environments and older adults might have leaned on their established careers and relationships as pillars of stability, emerging adults faced disruption to nearly every aspect of their developmental trajectory. This suggests that future crisis responses should consider stage-specific interventions – for instance, providing alternative career development opportunities for emerging adults. Further, these findings are important beyond an immediate pandemic context. As members of this cohort achieve traditional milestones of adulthood, such as establishing careers and starting families, understanding the impact of their pandemic experiences could explain potential variations or delays in these timelines.

Discussion

Chapter 8

General Discussion

8.1 Summary of Results

In this thesis, I investigated social disconnection in adolescence: its impact on cognition, the mitigating role of digital social interactions and its consequences for mental health and wellbeing. Below, I present a synthesis of my findings addressing the three overarching research questions that guided my investigation.

RQ1: What are the Effects of Social Disconnection?

This thesis presents findings on the effects of social disconnection from two main perspectives: acute, experimentally induced isolation in a lab setting, and real-world experiences of reduced social contact during the COVID-19 pandemic. Chapter 2 described the methodology of the experimental study involving acute social isolation in adolescents aged 16 – 19 years. Social isolation lasting just a few hours, regardless of access to digital social interactions, was found to induce significant changes in psychological state and cognitive processing compared to a baseline session. Participants reported **higher levels of state loneliness and boredom** after isolation compared to baseline, and **positive mood decreased**. Furthermore, isolation **heightened threat learning**. Specifically, adolescents showed marked increases in explicit threat discrimination (measured by the difference in self-reported arousal ratings to threat versus safety cues) after isolation compared to baseline. This increased discrimination was evident after the initial learning phase (acquisition) and remained partially elevated during subsequent phases (extinction and retention). There was also some evidence from implicit measures (electrodermal activity) showing elevated threat responding during extinction after isolation compared to baseline. These findings position isolation as a potential causal contributor to heightened threat vigilance.

As described in Chapter 3, acute social isolation also impacted reward responsiveness. Total isolation led to **increased social reward seeking** for large social rewards compared to isolation with digital social interactions. Participants also demonstrated increased reward learning after social isolation. This was evidenced by improved reward learning in the total isolation session compared to baseline and compared to isolation with digital social interactions, as measured by performance metrics including faster choice reaction times (RTs) and lower perseveration errors in the first reversal phase. However, it is important to note that there were no differences in performance accuracy between the sessions. Computational modelling further showed that after total isolation compared to baseline, participants had increased learning rates from positive feedback (both social and nonsocial). Participants also showed more reward exploitation (higher inverse temperature or *beta* parameter) after both isolation sessions compared to baseline for both social and nonsocial rewards. These results suggest that following isolation, adolescents placed more weight on each instance of feedback, particularly social feedback, to guide their behaviour. There was stronger evidence for the effect of isolation on learning from negative social feedback compared to positive social feedback.

While Chapter 4 does not directly investigate the effects of acute social isolation on reward-related brain function, it revealed how baseline neural reward sensitivity can predict subsequent reward-related behavioural responses to isolation. A significant correlation emerged between univariate neural reward sensitivity in the occipital cortex at baseline and reward seeking following isolation. Specifically, adolescents with lower baseline neural reward sensitivity demonstrated increased reward seeking after isolation. That there was no correlation between neural reward sensitivity and reward seeking behaviour at baseline suggests that neural reward sensitivity specifically predicts reward seeking behaviour in response to isolation rather than reward seeking generally.

In addition to well-controlled experiments, understanding the effects of social disconnection in naturalistic settings is essential for validating findings and establishing ecological validity. In the context of the real-world social disruptions caused by the COVID-19 pandemic, Chapter 6 indicated that late adolescents (18 – 25 years old) reported worsened mental health after the pandemic onset. This included a large **increase in self-reported depressive symptoms** and **worsening mental health** more generally. Participants also reported that there was a **reduction in their social needs being met** by their friends. Although loneliness levels in this sample during the pandemic were not significantly different from pre-pandemic samples of similar populations, this could be due to a potential ceiling effect, as this age group already reports high loneliness. Objective in-person social isolation, measured by smaller household size during the pandemic, was associated with **higher levels of loneliness** and **lower levels of happiness**, supporting results from the experimental study described in Chapter 2. In Chapter 7, qualitative

data from emerging adults (18 – 29) years old during the pandemic revealed prominent themes related to feelings of social isolation and loneliness due to social distancing mandates and relocation away from social networks. A significant concern that emerged was the **loss of opportunities**, particularly those related to key developmental goals for emerging adults such as gaining autonomy, developing identity and exploring relationships and career options, which were curtailed by restrictions on in-person interactions.

In summary, results from these studies indicate that social disconnection, ranging from acute experimental isolation to reduced real-world social contact, leads to increased subjective feelings of loneliness and boredom, decreased positive mood, heightened threat learning, and altered reward processing (including increased social reward seeking and changes in learning and exploration). In a real-world context of reduced social contact, it is also associated with worsened mental health (increased depressive symptoms, decreased happiness), decreased perception of social need fulfilment and disruption of developmental opportunities.

RQ2: Can Digital Social Interactions Remediate the Effects of Social Disconnection?

This research provides **mixed evidence** regarding the capacity of digital social interactions to remediate the effects of social disconnection. In the acute isolation experiment (Chapter 2), participants in the isolation session that allowed digital social interactions (iso-with-media) reported **lower levels of state loneliness and boredom** compared to the session of total social isolation (iso-total). This indicates that access to digital interactions helped to subjectively alleviate some negative feelings associated with isolation, though self-reported loneliness still increased compared to baseline in the iso-with-media session.

However, **access to digital social interactions did not significantly remediate the effects of isolation on threat learning**. There were no significant differences in explicit threat discrimination or implicit responses between the total isolation and the iso-with-media sessions. This suggests that while digital interactions may lessen subjective feelings of loneliness, they did not prevent the heightened threat learning observed after isolation. For reward responsiveness (Chapter 3), some aspects were differently affected by access to digital social interactions compared to total social isolation. Social reward seeking (measured by choice RTs) was faster in the iso-total session compared to the iso-with-media session for high social rewards, suggesting digital interactions led to slower social reward seeking. Although it is important to note that there were no differences in social reward seeking between iso-total and baseline. With regard to reward learning, perseveration errors (one measure of reward learning performance) were lower in the iso-total session compared to the iso-with-media session, suggesting that

perseveration was more severe when digital interactions were allowed. Reward exploitation (the beta parameter in the computational models) was higher after isolation with digital interactions compared to total social isolation. These findings suggest that **digital interactions might impact reward responsiveness differently than total isolation**, but not necessarily in a way that fully remediates the changes observed in total isolation; some aspects were "worse" (e.g., slower social reward seeking, increased perseveration) and some "better" (increased exploitation) within the narrow constraints of the reward learning task. It is noted that engaging in digital social interactions could alter the reinforcing nature of other social cues, potentially explaining differences in exploitation.

As described in the COVID-19 study in Chapter 6, the overall frequency of digital social interactions was not significantly associated with loneliness, depression or happiness among late adolescents. Despite the frequency of digital social interactions remaining stable, participants reported decreased feelings of connection derived from these digital social interactions during the pandemic compared to before. This suggests that digital social interactions, at least as spontaneously practised by participants in this study, did not effectively compensate for the loss of in-person contact in terms of mitigating loneliness or improving overall mental health (depression, happiness). However, the qualitative data on emotional experiences during the pandemic described in Chapter 7 did identify digital connections as a form of social support and an opportunity to reconnect with distant friends and relatives. Participants who described "gained opportunities" (which included these digital reconnections) reported better mental health outcomes (smaller increases in depression, less worsening of general mental health). This suggests that **specific positive uses of digital interactions might buffer against social disconnection**.

The systematic review (Chapter 5) provides further nuance regarding the potential benefits of one specific use of digital interactions – online self-disclosure. While online self-disclosure was generally perceived as less fulfilling for relationship quality compared to face-to-face interaction, the review found evidence that it offers unique benefits. Online interactions can be useful for bridging social capital, connecting across geographical distances, reaching a large number of people, and practising social skills for face-to-face communication (the "rehearsal hypothesis"). Specifically, **online self-disclosure appeared more beneficial for certain populations**, such as highly socially anxious youth (by providing information to reduce uncertainty about peers) and young boys aged 12 – 13 years (who showed a preference for online disclosure, which then seemed to stimulate later offline disclosure). When in-person socialising is limited (such as was the case during social distancing measures amid COVID-19), online social interactions might provide unique ways to deal with restrictions and help promote feelings of connectedness.

Overall, the empirical results suggest that while digital social interactions can partially alleviate subjective feelings of loneliness, they may not fully remediate the effects of social disconnection, such as heightened threat learning in response to acute social isolation or the overall negative subjective impact on mental health seen during COVID-19. However, digital interactions might offer specific, unique benefits related to social connection and skill development, particularly for certain individuals or purposes, and specific positive uses of digital social interaction might be linked with better mental health. The effectiveness of digital interactions for remediation likely depends on factors such as how digital platforms are used, the type and quality of the digital interaction, individual differences and the domain in question.

RQ3: How Might Social Disconnection Influence Mental Health and Well-being?

Given the evidence detailed in this thesis, I propose several potential ways social disconnection might influence mental health and wellbeing. One mechanism suggested by the experimental results in Chapter 2 is the link between state loneliness and **heightened threat learning**. Increased state loneliness during the acute isolation experiment was associated with increased explicit threat discrimination (the ability to distinguish between threat and safety cues). Loneliness is proposed as a potential mediator through which isolation affects threat learning. Heightened threat learning and vigilance, in turn, are well-established components of anxiety and threat-related disorders, implying that threat learning could indeed operate as a subsequent mechanism linking loneliness to mental illness. While the influence of unmeasured variables cannot be entirely excluded, the finding that loneliness statistically mediates a significant portion of isolation's effect on threat learning suggests a potential causal pathway.

Another potential pathway involves **changes in reward responsiveness**, discussed in Chapter 3. Increased state loneliness during isolation was correlated with increased social reward seeking (faster RTs for large social rewards) and increased learning from negative social feedback. The results suggest that loneliness might specifically drive *social* reward seeking. Social reward seeking might potentiate negative risk-taking behaviours, including drug use. The observation that participants showed increased learning from negative social feedback following isolation, especially those reporting greater loneliness, suggests a potential hypervigilance towards negative social cues, which aligns with findings related to threat learning and could impact mental health as it relates to conditions such as social anxiety. It is also critical to consider pre-existing individual differences when thinking about the mental health risks of social isolation. Low neural responsiveness to rewards has been linked to anhedonia (a reduced ability to experience pleasure; Nikolova et al., 2012; Southwick et al., 2005; Vidal-Ribas et al.,

2019). Anhedonia is a symptom associated with various mental health conditions, particularly depression. Given that lower neural reward sensitivity at baseline predicted increases in reward seeking after isolation (Chapter 4), reward related neural circuitry might be involved in the link between loneliness and depression.

Though correlational, the COVID-19 study described in Chapter 6 also provides real-world evidence linking social disconnection to negative mental health outcomes in a “natural experiment” characterised by dramatically reduced social contact. Adolescents reported significant increases in depression and decreases in happiness during a period characterised by reduced in-person social contact. Conversely, objective in-person social isolation (smaller household size) was associated with higher loneliness and lower happiness levels. This suggests that having fewer people physically present in one’s living environment during a period of widespread social restriction contributed to worse subjective wellbeing and increased feelings of loneliness. **Living with family** during this time appeared to be a protective factor against loneliness, potentially by providing a source of familial support. The decreased perception of social needs being met by friends during the pandemic also points to the impact of social disconnection on adolescents’ ability to feel that they are meeting their fundamental social needs. Further, qualitative data from the COVID-19 study described in Chapter 7 highlighted that **lost opportunities**, linked to key developmental goals (such as social exploration, gaining autonomy and establishing identity), due to restrictions on in-person interactions, were a prominent theme associated with reports of worsening mental health.

The systematic review on self-disclosure (Chapter 5) emphasises the positive link between adolescent self-disclosure and psychological wellbeing. Across studies, self-disclosure was found to predict life satisfaction. Engagement in self-disclosure can also be rewarding and allow for identity exploration, important factors in adolescent development. Conversely, **limited opportunities for relationship building through self-disclosure**, exacerbated by social disconnection, could negatively impact these aspects of wellbeing. While online self-disclosure might provide some opportunities for self-disclosure, the review also notes a negative effect in some circumstances. For example, regret from online self-disclosure, linked to frequent social media use and large/unfamiliar online networks, suggests a potential negative impact on mental wellbeing stemming from certain forms of digital social interactions.

In summary, my results suggest that social disconnection likely influences mental health and wellbeing in adolescents through multiple pathways, including heightened threat vigilance, and altered reward processing (potentially increasing seeking of social rewards and sensitivity to negative social cues). Amid social distancing restrictions during COVID-19, my research found that social disconnection was associated with self-reported decreases in happiness, increases in loneliness and decreases in feeling able to fulfil fundamental social needs. Additionally,

participants were critically concerned about lost opportunities (social and otherwise) crucial for development. Further, factors like familial support might act as protective buffers against some of the negative effects of social disconnection.

8.2 Considerations

There are several considerations to take into account when interpreting and drawing conclusions from the results of this thesis – including methodological and theoretical limitations (several are outlined below).

8.2.1 Theoretical Considerations

Nature of Digital Social Interactions. One of the most important theoretical considerations regarding the research in this thesis is related to the nature of digital social interactions. Whether digital social interactions fulfil social needs is debated (Novick et al., 2018) and some findings suggest the contrary, that is, that digital social interactions can increase loneliness (Nowland et al., 2018). However, the nature of digital interactions is likely an important factor. For instance, passive scrolling on social media might have different effects compared to active conversations via video call (Clark et al., 2018; Verduyn et al., 2017), and the identity and relationship between those in the interaction might also play a role. In the social isolation study (Chapters 2–4), some differences were observed in psychological state (loneliness and boredom) and some measures of reward responsiveness between total isolation and iso-with-media. However, only a few general self-report questions about digital social interactions during the iso-with-media session were included. Though the sample size was too small to explore psychological state, threat learning and reward responsiveness with regard to differences in digital social interactions, descriptive statistics about the digital social interactions participants engaged in during iso-with media are reported in the supplement. This consideration is also relevant to the study reported in Chapters 6–7. The type of digital social interaction practice (i.e., messaging, voice calling, video calling, etc.) and platform (i.e., Instagram, Whatsapp, etc.) used during COVID-19 likely altered the quality of social interaction, and it was not possible to separately examine frequency and feelings of connection for each type of digital social interaction.

Chronic Versus Acute Isolation and Loneliness. A second important theoretical consideration regards how the effects of isolation might be different depending on whether isolation and loneliness are acute versus chronic (Maes and Vanhalst, 2024). Chronic and state loneliness can

have opposite effects on social behaviour (Cacioppo and Cacioppo, 2018). The social homeostasis model (Holt-Lunstad and Sine, 2024) suggests that prolonged engagement of mechanisms intended for short-term adaptation to state loneliness can cause pathological states during chronic loneliness (Matthews and Tye, 2019). For example, acute loneliness might increase social motivation and encourage adaptive behaviours aimed at fostering social connections (Tomova et al., 2020), whereas chronic loneliness might diminish social motivation, leading to maladaptive behaviours and social disconnection (Holt-Lunstad et al., 2015). The social homeostasis model was proposed based on research on the effects of isolation in animal models, but similar theoretical frameworks have been proposed based on human research of chronic loneliness. For example, the cognitive control model of loneliness (Wong et al., 2022) similarly proposes that it is the prolonged engagement of regulatory mechanisms during loneliness that exhausts cognitive resources and results in aversive outcomes. Prolonged increases in reward responsiveness during chronic loneliness might ultimately result in imbalances of the reward system, increasing proneness to developing compulsive behaviours, or a blunting of reward system activity. Indeed, longitudinal studies in humans consistently link chronic loneliness to depression and substance use (Bonar et al., 2022; Dogan-Sander et al., 2021; Essau et al., 2020; Goosby et al., 2013; Hawkley and Capitanio, 2015; Kayaoğlu et al., 2022; Ladd and Ettekal, 2013; Ozeylem et al., 2021; Prinstein and La Greca, 2002; Qualter et al., 2013). Whether the experimental findings presented in this thesis can be translated to the effects of real-life chronic loneliness and how threat learning and reward responsiveness might be differentially affected by chronic versus acute loneliness remains to be explored. Further, while state loneliness is proposed as a potential mechanism underlying the impact of isolation on threat learning and reward responsiveness (as reported in Chapters 2–3), it must be acknowledged that definitive causal claims about any mediators cannot be made.

Individual Differences. The relationship between loneliness and isolation is likely complex, and might vary between individuals with different personality types or mental health conditions and across different contexts (e.g., social versus nonsocial settings; Towner et al., 2023; Bu et al., 2020; Card and Skakoon-Sparling, 2023). The processes investigated in this thesis might be particularly relevant for clinical populations. For example, these processes might look different for those affected by mental health disorders. It is important to note that the social isolation study (Chapters 2–4) focused on healthy adolescents without pre-existing mental health conditions. It is possible that the observed effects of isolation would be more pronounced in individuals already prone to anxiety and depression or those experiencing chronic loneliness. Moreover, there might be substantial individual differences in the amount of social connection needed to prevent loneliness and this individual variability might have

implications for long-term well-being. Additionally, the role of digital social interactions might depend on an individual's in-person social network.

8.2.2 Methodological Limitations

Measurement. A foundational part of science is defining and measuring what is being studied (Flake and Fried, 2020). However, in psychological science, this poses a challenge because psychological constructs such as depression or cognitive processes are often not directly observable and measures designed to assess the same or related constructs sometimes yield divergent results. For example, in Chapter 2 threat learning was measured using both explicit (subjective responses) and implicit measures (electrodermal activity). While explicit measures of threat learning showed clear effects, implicit measures were weaker (although still significant). Subjective responses are standard in threat learning paradigms and have shown good validity (studies have found differences in threat learning as measured by subjective responses between participants with anxiety versus healthy comparison participants; Craske et al., 2008; Shechner et al., 2015; Waters and Pine, 2016). However, with all self-report ratings there is a possibility that participants might have been affected by things like social desirability or demand characteristics.

Further, it is impossible to investigate all relevant constructs in a single study. For example, it cannot be ruled out that the observed effects in the social isolation study (Chapters 2–3) might have been partially driven by other (unmeasured) variables in addition to loneliness, such as fatigue or energetic arousal. Researchers have identified two distinct dimensions of arousal: anxious arousal, ranging from calmness to anxiety, and energetic arousal, ranging from tiredness to energy (Dickman, 2002). A recent study in adults found that social isolation led to decreased energetic arousal and increased fatigue in both laboratory and field settings (Stijovic et al., 2023). The reward-related findings presented in Chapter 3 should be considered in light of research demonstrating an association between low arousal and decreased motivation (Berridge and Arnsten, 2013). However, given the increased reward responsiveness indicative of enhanced motivation reported in Chapter 3, it seems unlikely that isolation-induced decreases in arousal would drive the observed pattern of results.

Generalisability. Data collection for the empirical studies presented in this thesis took place during various stages of the COVID-19 pandemic. COVID-19, a novel coronavirus, was first identified in Wuhan, China in December 2019 before being declared a global pandemic on the 11th of March, 2020. Authorities worldwide imposed lockdowns, travel restrictions, contact tracing, and other measures which severely disrupted social, personal and professional life. For the study discussed in Chapters 6–7, data collection commenced on the 28th of April 2020 and

concluded on the 4th of June. This study was conducted in collaboration with researchers at the University of California, Los Angeles (UCLA) in the United States. The majority of the sample (77%) were located in California at the time of the survey, a further 16% of participants were located in other states in the United States, 5% of participants were internationally located, and 2% did not answer this question. On the 10th of March 2020 UCLA suspended in-person classes for the remainder of the winter quarter and students were encouraged to begin the spring quarter from home. As the COVID-19 situation progressed, students were encouraged to remain home after spring break if possible, and remote instruction was extended through Spring 2021. A stay-at-home order was imposed in California on the 19th of March 2020 that was not lifted until the 25th of January 2021. As such, social distancing guidance/mandates in California remained comparable for the duration of data collection for this study.

The social isolation study (Chapters 2–4) commenced data collection in April 2021 (in Cambridge [U.K.]) a period marked by fluctuating social restrictions which might have influenced participants' baseline levels of social isolation. Despite ongoing social distancing measures, the majority of participants in the study were experiencing some degree of in-person social interaction at the time of testing (schools in England had reopened by this time). Nonetheless, the effect of the experimental isolation manipulation might be amplified in a post-pandemic context in which higher levels of in person social contact occurs.

In the experimental study of social isolation discussed in Chapters 2–4 the sample was a relatively small, demographically homogenous, socially connected group of adolescents aged 16 – 19 years without diagnosed mental health conditions living near Cambridge, U.K. Due to the study's screening criteria, participants could not exhibit high levels of chronic loneliness or have a significantly smaller social network compared to a typical adolescent sample. This approach was implemented in order to avoid exposing vulnerable young people to potentially distressing isolation and to prevent conflating the effects of acute and chronic isolation. Consequently, the sample was likely biased towards non-lonely adolescents with higher social motivation, limiting the generalisability of these findings to other populations. Similarly, while the participants in the study described in Chapters 6–7 were ethnically and racially diverse, the sample consisted primarily of female university students from UCLA. Therefore, these results might not generalise to more diverse populations or countries and cultures not included in the study's sample.

Further, it is important to consider whether the findings presented generalise to other age groups. The studies in this thesis examined different age ranges within the adolescent period with some overlap. Therefore, it is not certain whether these results are unique to adolescents specifically. Further, in both empirical studies, data was collected only on a narrow set of mental health dimensions. For example, in Chapter 7, I only analysed how qualitative experiences

mapped on to two dimensions of mental health in this paper (depressive symptoms and general change in mental health). Therefore, findings cannot be generalised to other types of mental health disorders or challenges that participants might have been facing amid pandemic-related social disconnection.

Cross-Sectional Data. The data presented in this thesis was in large part cross-sectional, meaning that results cannot be extrapolated to make inferences about potential long term effects. This might be particularly relevant for processes like long-term threat learning retention discussed in Chapter 2. Further, in the study discussed in Chapters 6–7 the cross-sectional design did not allow strong claims to be made about baseline levels of digital social interaction, loneliness, depression and happiness before the onset of the COVID-19 pandemic and instead relied on retrospective reports (i.e, asking participants to reflect on their mental health from before the pandemic). Therefore, it is not possible to rule out bias in these retrospective reports.

Order Effects. The social isolation study (Chapters 2–4) began with a baseline assessment of each participant. This design allowed the examination of the impacts of isolation relative to an unaffected baseline as well as the use of baseline neural reward sensitivity as a predictor of isolation-induced reward responsiveness. However, as the baseline was always completed first, there is the possibility that the isolation results presented are due to order effects. The two isolation sessions (iso-with-media and iso-total) were counterbalanced, however, which allowed sensitivity analyses to be conducted to examine whether order effects between the two sessions played a role in the findings reported in this chapter. Sensitivity analyses did not suggest that order played a role in any of our results (see the supplement for details).

8.3 Future Directions

Given the considerations outlined above, there are several concrete opportunities for refining and extending the work in this thesis. To better understand the effects of digital social interactions, future research should differentiate between various digital communication practices. For example, studies should compare the effects of passively viewing content versus actively engaging in conversations, and distinguish between the broad use of social media platforms and focused interactions through messaging applications. Differences between chronic and acute isolation merit further investigation and research should examine the long-term impacts of social disconnection. For example, studies could longitudinally track individuals who experienced COVID-19-related social disconnection to determine whether this disruption during sensitive windows of development influenced long-term mental health trajectories. Additionally, investi-

gations should evaluate interventions designed to provide alternative pathways for achieving developmental milestones during times of crisis. Individual differences remain another critical area for exploration. Future research should prioritise the inclusion of diverse populations, such as those experiencing chronic loneliness, individuals with varying personality traits, those with mental health conditions and age groups with lower social motivation compared to typically highly socially motivated adolescents. Additionally, comparative studies across developmental stages could determine whether the effects observed are adolescent-specific or generalise to other age groups. Future studies should also distinctly measure how isolation affects both anxious and energetic arousal and investigate how these dimensions relate to threat learning and reward responsiveness. Similarly, the relationship between loneliness, boredom and cognitive processes requires deeper investigation, particularly as these constructs showed some opposing effects in our research. Social learning processes, particularly in threat domains, warrant further investigation. While research has examined how children and adolescents learn about threats from parents versus unfamiliar adults (Silvers et al., 2021; Skversky-Blocq et al., 2021a,b), studies should explore developmental changes in vicarious threat learning and how adolescents acquire threat information from peers compared to adults, especially in contexts of social disconnection. Finally, methodological refinements to the experimental manipulation of social isolation used in this thesis could strengthen causal claims about isolation effects in humans. Future research should implement fully counterbalanced designs across all experimental sessions, including baseline, and consider incorporating natural or enhanced social interaction sessions as additional comparison conditions. Beyond these improvements and extensions, this thesis highlights several broader open questions that could define future research programmes. A few of these are expanded upon below.

8.3.1 Social Isolation in the Brain

Future research would benefit from using neuroimaging to explore isolation-induced changes in threat and reward processing. A recent study found that acute social isolation in adult humans evoked a social craving response in the midbrain, similar to how food fasting evoked hunger and food craving (Tomova et al., 2020), suggesting that social deprivation leads to social craving analogously to the way food deprivation leads to food craving. While altered activity in threat and reward related circuitry has been consistently shown in animal model studies of adolescent isolation (Guadagno et al., 2018; Hall, 1998; Novick et al., 2018; Zhang et al., 2012), direct experimental assessment of threat and reward circuit activity following isolation in adolescent humans would provide further evidence of isolation-induced effects. Future research investigating the neural mechanisms underlying threat learning after social

isolation could provide valuable insights about the divergence of explicit and implicit threat learning responses.

Structural analyses could also provide important insight. For example, future studies should examine structural differences as predictors of sensitivity to social isolation. Brain microstructure also represents an exciting avenue for future neuroscience research in human adolescents. An experimental study in rodents found that changes in sensitivity to social reward learning corresponded to developmental downregulation of synaptic plasticity in the nucleus accumbens (Nardou et al., 2019), and that increasing plasticity (through drug-induced upregulation of oxytocin) reinstated adolescent levels of sensitivity to social reward learning in adult rats. Investigating myelination using microstructural methods could help investigate sensitive periods for social connection during adolescence in humans.

8.3.2 Digital Fulfilment of Social Needs

A key area for future research involves delving deeper into the potential of digital social interactions to fulfil social needs. Whether digital social interactions fulfil social needs is debated and some findings suggest the contrary, that is, that digital social interactions can increase loneliness (Bayindir and Paisley, 2019). The studies presented in this thesis (Chapters 2–3) showed that during isolation with access to digital social interactions, participants self-reported lower feelings of state loneliness compared to total isolation. However, results with regard to threat learning and reward responsiveness were mixed. Thus, the findings in this thesis provide partial support for the potential of digital social interactions to fulfil social needs.

The systematic review discussed in Chapter 5 highlighted the role of self-disclosure for satisfying social needs of adolescents and has shown that online self-disclosure can complement face-to-face self-disclosure. However, this review revealed that only few studies compared different types of self-disclosure outside the comparison of online versus offline self-disclosure. Only one study compared intimate versus superficial self-disclosure in adolescent girls and found that superficial self-disclosure might have a unique role in adolescent social interactions as it was experienced as rewarding and adolescents preferred to engage in it more compared to intimate self-disclosure which carries more risk of rejection. Future studies should compare the role of intimate versus superficial self-disclosure in more detail and also assess the effects of gender and age. Future research should assess self-disclosure in boys and girls early in adolescence and follow their development into their late teens to understand the role of (online and offline) self-disclosure with regard to the fulfilment of social needs.

In my future research, I am particularly passionate about employing theory-driven experimental methods informed by translational research between animal and human models to investigate the impact of digital social interactions on wellbeing. Recent animal studies

offer compelling neural targets for investigation in humans. Given that social connections are fundamental to survival across species, researchers have hypothesised that evolutionarily conserved neural systems underlie the maintenance of social connections (Matthews and Tye, 2019). Supporting this, Liu et al. (2025) recently identified two distinct neuronal populations in the mouse hypothalamus activated by social isolation and subsequent social contact, potentially reflecting neural representations of social need and social satiety. Notably, a recent study (Kim et al., 2024) provided the first evidence that the human hypothalamus, much like its animal counterpart, encodes and coordinates strategic survival behaviours. Building on these findings, adopting an acute social isolation paradigm (such as the one used in this thesis) could enable investigation of whether the human hypothalamus encodes states of social need and social satiety, as observed in animal models, and how digital social interactions might modulate these responses. Such an approach could provide neural evidence regarding the extent to which digital social interactions fulfil social needs.

8.3.3 Social Media

Social media use has become virtually universal, particularly among younger demographics. More than one-third of the 95% of adolescent social media users aged 13 – 17 in the U.S. describe their usage as "almost constant" (Advisory, 2023). Despite most platforms setting 13 as the minimum required age, nearly 40% of children between 8 – 12 years also engage with social media (Advisory, 2023). The substantial global reach of social media is demonstrated by the 3.4 billion users recorded in 2019, with growth continuing at an estimated annual rate of 9% (Koh et al., 2024).

The relationship between social media use and mental health is intricate, likely bidirectional and multifaceted (Meier and Reinecke, 2021; Odgers, 2024; Valkenburg et al., 2022). Given this, future studies should experimentally investigate how individuals are impacted by social media. I am particularly interested in understanding the effects of social media feedback (e.g., comments, messages, etc.) on adolescents. While positive social feedback can be rewarding (Izuma et al., 2008), toxic digital social interactions pose growing and significant concerns and a recent paper proposed that features of social media might intensify how negative feedback is internalised (with potential adverse effects on wellbeing; Pandita et al., 2024). Separately, scientists have begun to computationally model the dynamics of subjective states such as mood (Eldar et al., 2016) and self-esteem (Low et al., 2022) using a reinforcement learning framework. These computational approaches offer promising tools for investigating how social media feedback might dynamically regulate psychological states, particularly because differences in computational parameters of reinforcement learning have been observed in a number of psychiatric disorders (Hauser et al., 2019). Further, these constructs have shown interesting

brain-behaviour correlations. In emerging adults, Da Silva Pinho et al. (2024) demonstrated that computational measures of sensitivity to social media feedback correlated with individual differences in subcortical-limbic brain structure. It would be interesting to use functional imaging approaches (such as multivariate pattern analysis) to investigate whether exposure to social media feedback can alter neural representations of self-esteem (Guassi Moreira et al., 2023; Stendel et al., 2024).

Relatedly, Chapter 5 revealed that only one study assessed negative effects of self-disclosure which was measured as regret of posting information about oneself. This study found that particularly young people who use social media often and have large (anonymous) friend groups on social media tend to experience regret more often. More research is needed on the potentially negative effects of disclosing information about oneself online (particularly via social media) and how these effects affect mental well-being of young people. In addition, it would be beneficial to conduct qualitative research to identify the ways in which different social media platforms (e.g., Instagram, TikTok, WhatsApp, Facebook, etc.) are used and how their unique features might contribute to feelings of social connection (Yeshua-Katz et al., 2021).

8.4 Concluding Remarks

In conclusion, this thesis demonstrates the significant impact of social disconnection on adolescents' psychological state and cognition, particularly threat learning and reward responsiveness. While digital social interactions may partially alleviate subjective feelings of loneliness, their ability to mitigate the broader effects of social isolation – including negative mental health outcomes – remains uncertain. The research presented in this thesis highlights the complex relationship between social connection, digital engagement and adolescent wellbeing. Although digital platforms offer abundant opportunities for social interaction, these might compromise meaningful social connection, especially during this developmentally sensitive window. Understanding adolescent digital social interaction requires a detailed insight into its use, recognising individual differences and the distinct characteristics of various platforms and practices. It is well established that social isolation and loneliness adversely affect physical and psychological health. However, the research in this thesis offers initial insights into *why* this might be the case. Addressing social disconnection requires continued research that: investigates theoretically driven mechanisms potentially linking social disconnection to mental ill health; conducts longitudinal studies following individuals across the lifespan; examines digital social interactions while differentiating between types of digital social contact; and employs robust methodologies (such as experimental manipulations). Ultimately, the work in

this thesis provides foundational knowledge that I hope will inform the creation of interventions to foster resilient adolescent development and promote genuine social connection.

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