Friend Request Accepted: Fundamental Features of Social Environments Determine Social Affiliation Decisions

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Contents

Abstract: Humans start new friendships and social connections throughout their lives, and it has been consistently found that such relationships lead to mental and physical well-being. In this thesis, I investigated the behavioural and neural mechanisms governing our decisions to initiate friendships with other people. I examined whether such decisions are influenced by the friendliness, i.e., the social reward rate, and the density, i.e., the rate of opportunities, afforded by the environment. In a computer based online task (n=783), I found that people were more likely to send friend requests in friendly and sparse environments in comparison to hostile and dense environments. Further, I found task-related measures like overall friend requests were correlated with personality-related factors like social thriving. Next, in a 7T fMRI study (n=24), I found that the subcortical dorsal raphe nucleus represented density-related effects and the substantia nigra (SN) represented friendliness-related effects. Further, cortical regions like the anterior insula (aI) represented both friendliness and density related effects. Next, in resting state fMRI data (n=400), I showed that model predicted factor score corresponding to anhedonia was related to functional connectivity between the SN and the aI. Finally, in a social learning task, I found that people took background statistics of an environment into account when deciding between learning from others and foraging for food by themselves. Taken together, these findings suggest that the human brain takes background statistics of an environment into account while making social decisions and that such decisions can be explained by personality or psychiatric factors.

Chapter 1

Introduction

> "I wish I had stayed in touch with my friends."
>
> —*Top Five Regrets of the Dying (Ware, 2012)*

No one is a stranger to the warm feeling of connecting with people we love. Be it when dining with friends or be it when unwinding with family — social connection rarely fails to spark joy. The cliche is that humans are social animals, and scientific evidence seems to concur. Those of us who thrive socially often benefit from longer, happier, and healthier lives. On the flipside, loneliness and social isolation are distasteful experiences to say the least, and can also carry physical or mental health risks. Indeed, as the opening quote suggests, not staying in touch with friends might be a top regret of the dying.

While the benefits of social connection are many, forming and maintaining social connections is not without its challenges. People frequently relocate to pursue their educational or career ambitions, often leaving behind established social circles and needing to build new ones from scratch. While social media may have made it easier to stay in touch with old friends, it may also have inadvertently discouraged efforts to gather in-person. An entire generation has been raised socialising online, and its effect on mental health are raising concern. Moreover recently, an unprecedented pandemic forced many into social isolation for months at a time, and the effects of such isolation on our well-being are still unfolding.

In this thesis, I will study human decisions to form social connections with others. Specifically, I will examine how features of one's environment—for instance, whether meeting at a park full of people, or at a workplace with friendly faces—shapes social decisions. I will then examine how such decisions of social affiliation relate to our mental health. Finally, I will investigate the neural connections that support such social decisions.

In chapter two, I will provide a theoretical background of the psychology and neuroscience of social connection. I will start by describing classical social psychology studies on interpersonal connections, including the link between social thriving and health, physical or mental. Next, I will provide a broad overview of the neuroscience of social cognition. I will describe theories such as the social brain hypothesis, which is the idea that our brains have evolved to meet social demands, and classical studies in social neuroscience like those that describe how the brain represents ourselves and others, how we infer mental states of others, and how we use facial expressions to recognise emotions in others.

From chapter three onward, I will present experimental findings. In chapter three, I will present a study in which people make decisions of friendship formation in different environmental contexts. I will describe a novel social decision-making task—henceforth, the friend request task—in which people send friendship requests to people in different environmental contexts. I will show that features of the background environment, like how friendly people are in each environment, or how many people occupy a given environment, influence our choices of initiating friendships with others.

In chapter four, I will then link decisions of social affiliation to one's mental health and personality profile. I will use data-driven methodologies like factor analysis to construct participant psychiatric and personality profile, reducing several mental health symptoms into fewer dimensions that share variance. Then, I will examine how one's social decisions might relate to these personality and psychiatric factors.

In chapter five, I will examine the neural basis of social affiliation decisions. Using high field 7 Tesla (7T) neuroimaging, I will describe how social affiliation decisions, and the contexts in which they are undertaken, are encoded in pre-defined regions of interest. I will also examine whether these regions of interest demonstrate any functional connectivity that is related to the making of social affiliation decisions.

Equipped with the psychiatric factors and neural networks that are linked to social affiliation decisions, in chapter six, I will examine whether one's psychiatric factors can explain functional connectivity at rest. I will use a large-scale database of 7T resting state functional magnetic resonance imaging from the Human Connectome Project to test for a relationship between individual variation in functional connectivity in the brain and individual variation in psychiatric factors. I will also examine the link between psychiatric factors like social thriving and anatomical features of the brain like white matter connectivity.

Finally, in chapter seven, I will present exploratory findings from a novel task involving a different kind of social decision: whether to learn from others or pursue independent exploration in foraging environments. In a manner similar to the friend request studies, I will examine the link between social foraging decisions and one's personality and psychiatric profile.

In this chapter, I will review studies on the psychology and neuroscience of social connection. In section one, I will describe the importance of social connection and its impact on our physical and mental health. Here, I will review studies which show people with larger social networks live longer lives, and those without carry higher risks of mortality and heart diseases. I will review literature examining whether social connection is a fundamental need and do experiences in early childhood explain relationships we form as adults. Next, I will describe studies outlining the factors that lead to formation of social bonds—namely similarity, proximity, familiarity, and physical attractiveness. I will also examine science's take on the age-old question: do looks matter?

In section two, I will broadly describe the neuroscience of social cognition. Here I will examine classical studies on self vs other representation, and studies on how we infer mental states of others. I will describe how parts of the brain like the amygdala help infer emotions from facial expression of others, how dopaminergic systems might encode social rewards, and how the orbitofrontal cortex might prevent us from committing a social faux pas.

In section three, I will review the brain regions that might represent decisions made in different social environments. I will first outline the theoretical background of foraging studies that might help inform hypotheses about the neural circuits involved in representing social environments. Based on these studies, I will then name 7 brain regions of interest for my study: the dorsal raphe nucleus, lateral habenula, substantia nigra, ventral tegmental area, hypothalamus, anterior insula, and the dorsomedial prefrontal cortex. I will describe the functions of these regions in general, and why they may be involved in encoding social contexts in particular.

Finally, in section four, I will talk about mental health. Social connection is related to mental health, but how so remains a matter of continuous study. In this section I will outline the various methods of classification of mental illnesses, and the illnesses themselves that they describe. I will present the research regarding the diagnosis, neurobiology, and treatment of various mental health conditions. I will end this section with a discussion on the role of social media in influencing mental health, particularly for young adults.

1.1 The Social psychology of interpersonal relationships

Social Ties and Psychological Well-being

Studies in social psychology have consistently found that having more and deeper social ties leads to happiness and well-being. In a review of the major sources of happiness, Diener (1984) identified social contact as an important contributor to subjective well-being. For instance, several studies showed a correlation between objective measures of social activity (like participation in social events) and subjective well-being. In addition, longitudinal studies have found that increases or decreases in social ties led to concurrent changes in subjective happiness (Bradburn, 1969). The influence of social connection on happiness held even when health and other factors were controlled for. Further, a large social network led to happiness whereas social isolation induced feelings of loneliness and depression (Kawachi and Berkman, 2001).

Romantic relationships, in particular, contribute significantly towards feelings of happiness and well-being. For instance, Easterlin (2003) suggested that people in satisfying romantic relationships tend to be happier than their single counterparts, and divorce generally led to a sharp decrease in happiness. However, this did not mean that simply getting married made people happier. It is possible that people who were happier in the first place were more likely to initiate romantic connections. In support of this idea, Harker and Keltner (2001) found that expressions of positive emotion in women's college yearbook pictures predicted marriage success up to 30 years later. These findings held true even after controlling for factors like physical attractiveness and social desirability.

Social Ties and Physical Well-being

While it is intuitive to think that relationships affect our psychological well-being, the connection between relationships and physical well-being is perhaps more surprising. For instance, Williams et al. (1992) found that unmarried patients without a confidant had significantly lower chances of survival five years after suffering from a heart attack than patients who were either married or had a confidant. Further, Rohrbaugh et al. (2006) showed that the quality of a marriage predicted chances of survival after an 8-year period following an episode of heart failure.

The beneficial effects of social relationships were not limited to people with severe illnesses. In a classic study, Berkman and Syme (1979) found that in a random sample of the population, people who had more social and community ties (measured in terms of degree of contact with friends, relatives, romantic partners, church affiliation, etc.) were two to three times more likely to remain alive nine years later compared to those who lacked such ties. Further, they found that the association between social ties and mortality was independent of physical health (self-reported), socioeconomic status, and health-influencing practices like smoking, alcohol consumption, physical activity, and utilisation of preventive health services.

Inspired by the growing evidence on the relationship between social relationships and mortality, Cacioppo and Cacioppo (2014a) decided to focus on one particular facet of social connection — the degree to which one feels lonely. They found that loneliness heightened sensitivity to social threat and motivated people to renew their social connections. They also found that loneliness impaired executive functions, sleep, mental and physical well-being. These effects contributed to a higher risk of morbidity and mortality in lonely older adults.

The Need to Belong

The studies discussed thus far have indicated social affiliation of any kind has numerous benefits for our physical and mental health. Based on such findings, Baumeister and Leary (1995) proposed that people have a fundamental need to belong. They examined various criteria necessary for any drive to be considered a need (e.g. a fundamental need should produce effects readily in all but adverse situations, it should apply to all people irrespective of culture, etc.) and concluded that our desire to affiliate with others met all the criteria.

Baumeister and Leary (1995) argued that a fundamental need to belong evolved in humans as a consequence of natural selection. In our evolutionary past, people must have depended on others for a variety of basic needs like food, water, and shelter. By living with others, people could share food and help care for offspring. Survival tasks like hunting large animals or defense against predatory animals were also best achieved in groups. Children who stayed with adults were more likely to survive as they were more likely to receive care, food, and security.

In the animal kingdom, Testard et al. (2024) studied macaque monkeys living in Cayo Santiago, a small island off the coast of Puerto Rico. During the course of the study, the island was hit by a hurricane. The researchers found that the animals that were more likely to be socially tolerant—more co-operative, less aggressive—were also more likely to survive the aftermath of the hurricane.

This "need to belong" hypothesis is supported by studies showing that humans form social bonds relatively easily even in the absence of conducive circumstances. For instance, cross cultural studies have shown that people across all societies belong to groups that involve face-to-face interactions (Baumeister and Leary, 1995). The Robbers Cave study showed that when previously unacquainted boys were randomly assigned to new groups, they formed strong loyalties and group identification ties (Sherif et al., 1961). When in groups, people showed a strong preference for their team-mates, a phenomenon called the in-group bias (Spears and Taushch, 2021). This bias was prominent even in groups where members were completely anonymous to each other, had no face-to-face interactions, and had no self-interest at stake (Tajfel et al., 1971).

Finally, babies preferred looking at human faces, even at 30 minutes old, compared to equally complex alternative stimuli. For example, Goren et al. (1975) presented 40 newborn infants (median age 9 minutes) with a moving stimulus which was either a face, a "scrambled" version of a face, or a blank head outline. Analysing head and eye movements, they found that babies showed a strong responsiveness to faces compared to other stimuli. Based on these observations, the authors suggested that a preference to look at faces might be an innate feature in human neonates. This finding, however, has faced problems with replication. For instance, Johnson et al. (1991) suggested that babies around 1 month old do not show any preference for faces.

The need to belong hypothesis would suggest that there is a satiation point for friendships. After the need for connection is met, we might not want to initiate more social affiliation. Such a way of conceptualising the need to belong would be consistent with Dunbar's number—the idea that, on average, different people have similar needs for a small number of close friends and larger number of more distant acquaintances—an idea which is explained in detail in the section on the social brain hypothesis.[1].

Attachment Theory

While Baumeister and Leary (1995)'s need to belong hypothesis suggests that we have a fundamental need to belong, which is met by contact with any human, Bowlby (1982)'s attachment theory emphasises the significance of one particular connection: the one between parent (or caregiver) and child. According to attachment theory, childhood experiences with the primary caregiver (the mother in most instances) shape our expectations about how relationships function, and consequently influence our behaviour in adult relationships.

Based on early experiences with their primary caregivers, people develop various styles of attachment. Hazan and Shaver (1987) proposed that people can generally be classified into three categories: secure, avoidant, and anxious. The researchers suggested that individuals who had stable caregivers in their childhood developed a secure attachment style later in life. Such children generally viewed themselves positively, and others as friendly and trustworthy. In contrast, infants who had unresponsive or unsupportive caregivers were more likely to develop one of the two insecure attachment styles: anxious or avoidant. People with an avoidant attachment style tended to avoid intimacy because they did not view others as trustworthy. On the other hand, people with an anxious attachment style lacked self-confidence and were more inclined to worry about the stability of their relationships.

Karremans and Finkenauer (2021) noted that contemporary research viewed attachment styles differently from the classic three-styles model. Rather than conceptualising attachment styles as discrete categories, it instead interpreted them along two continuous dimensions: the degree to which one was anxious about being abandoned, and the degree to which one tended to avoid intimacy. People with secure attachment styles scored low on both dimensions.

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[1] the-social-brain-hypothesis

Several studies have suggested that attachment styles do indeed impact people's behaviour in adult relationships. For example, Feeney (2002) found that secure people reported a higher satisfaction in their romantic relationships. Similarly, Kafetsios and Nezlek (2002) found that secure people reported greater satisfaction in their friendships and other non-romantic relationships.

Initiating Relationships

Proximity

Having established the importance of social connection, we now examine the factors that determine how friendships start. According to studies in social psychology, four factors contribute considerably to friendship formation: proximity, familiarity, similarity, and physical attractiveness.

When moving into a new city, we might be tempted to find a remote location that is quiet and idle, hoping to get a silent night's sleep or catch a relaxed evening. However, if forming new social connections were a priority, then being away from people may reduce our likelihood of making friends. Several studies show that proximity, that is being physically close to others, increases our chances of making friends.

Festinger et al. (1950) undertook a pioneering study that highlighted the power of proximity. They examined how friendships developed amongst a sample of 260 married student couples over the course of 10 months. These couples were assigned an apartment in a housing complex containing several multi-floor buildings. The authors found that physical proximity best predicted the development of friendships. For instance, people were more likely to befriend people living on the same floor, and they were more likely to befriend their next-door neighbour in comparison to those living far across the corridor. On the contrary, people also showed an increased dislike for people in their proximity. Thus, it appears that proximity is polarising: it helps us connect which may lead to a friendship, but may also lead to resentment.

Another striking example of the power of proximity comes from a study by

Back et al. (2008). The authors tracked the development of friendships in a cohort of incoming psychology students over the first year of their study. At first, the researchers assigned these students to random seat numbers. They then asked each student to introduce themselves. Immediately after each introduction, every other student answered two questions: how much did they like the person that just introduced themselves, and how much would they like to meet that person. These scores were then aggregated to form a combined 'friendship intensity' measure. After a year, they showed each student photographs of people from the first meeting, and asked them the same questions. Students who sat next to each other were found to have a higher friendship intensity scores than students who sat in the same row. Further students who sat in the same row had higher scores than those seated without any noteworthy proximity. These results held even after the scores were collected a year later. The authors concluded that friendship might be created simply by chance because people drew the "right random number", highlighting the role of proximity in making connections.

Familiarity

Another factor that facilitates social affiliation is familiarity. Mere exposure to people, or to symbols for that matter, is known to increase our positive affect toward those people or stimuli (Bornstein, 1989).

In a classic study, Moreland and Beach (1992) showed that mere exposure led to likability. In the study, the researchers asked four women of similar appearance to attend a large college course, but each for a different number of sessions (0, 5, 10, or 15 sessions). Further, these women were explicitly instructed to avoid interacting with the students. At the end of the term, students were shown photographs of the four women and asked to rate them on scales of familiarity, similarity, and affinity. The researchers found that mere exposure had weak effects on familiarity, but stronger effects on similarity and affinity. In other words, people liked others following mere exposure, despite not being conscious of the familiarity.

Another phenomenon is that people find “average faces” more attractive than more distinctive faces. One interpretation of this finding is that an average face is one that is likely to resemble our overall experience. In this sense the finding might also, albeit more indirectly, be taken as support for the idea that we like people who are familiar to us. Langlois and Roggman (1990) took a sample of 96 digital faces of men and women each (which included Hispanic and Asian faces) and divided them into two sets of 32 faces, from which they created six composite faces by mathematically averaging them. They then asked undergraduate students to rate the physical attractiveness of both the original faces and the composites. They found that heavily averaged faces were rated significantly more attractive than original faces. This finding might indirectly suggest that we may readily like people who we recognise compared to people who are unusual or rare.

Similarity

Empirical studies have showed that we like people who are like us, a phenomenon often called the similarity-attraction effect (Karremans and Finkenauer, 2021). For instance, Byrne et al. (1971) recruited 20 male and 20 female students from a summer session in a course in introductory psychology. Each of these students participated in an experiment with two confederates of the same sex, introduced to them as students from another psychology course. Each participant was given a 24-item Survey of Attitudes, a scale comprising topics ranging from preferences of music to beliefs about God. Prior to every session, one of the confederates was asked to agree with the subject on all but two topics, while the other confederate was to do the opposite: disagree on all but two topics. By manipulating the draw, it was arranged that the participant would always go first, while the order of the two confederates was counterbalanced. After everyone shared their views, the participant was asked to fill the Interpersonal Judgement Scale as a measure of interpersonal liking. Whether the participant sat close to either of the confederates during the debriefing session was also taken as a measure of interpersonal liking. The researchers found that people were more attracted to similar than to dissimilar strangers, and that men were more likely to sit across men whereas women were more likely to sit across women.

Not only does similarity lead to affiliation, but intriguingly, affiliation might also lead to similarity. For example, marital partners are showed to become more similar over time (Berscheid and Reis, 1998). Gruber-Baldini et al. (1995) found that spouses became similar in their verbal and intellectual abilities over a 14-year period and attitudinal flexibility over a 21-year period.

Interestingly, the similarity-attraction effect might work even if the similarity is perceived and not actual (Karremans and Finkenauer, 2021). Montoya et al. (2008) analysed over 300 laboratory and field studies and found that while both actual and perceived similarity led to attraction, the effect of actual similarity was lower in studies that involved face-to-face interactions. In addition, after accounting for perceived similarity, the effect of actual similarity in existing relationships was not significant.

Why do we like people who are similar to us? Karremans and Finkenauer (2021) suggested that people similar to us are more rewarding because they validate our views, thoughts, and opinions, which in turn makes us feel good. Within the context of a relationship, similar partners are more likely to accept each other as they are, and are therefore able to gratify each other's needs. Murray et al. (2002) argued that intimate partners may find a sense of belonging by assuming that their partners were mirrors of themselves. While the mechanism remains a matter of ongoing research, the finding that similarity leads to attraction is in itself found to be robust.

Physical Attractiveness

Often, the first impression we have of someone is based on their physical appearance. Several studies have shown that we judge physically attractive people more favourably. For instance, Chaiken (1979) showed that attractive people are more likely to raise money for charity than unattractive people. Downs and Lyons (1991) found that courtroom judges were more likely to fine lower amounts for misdemeanour to attractive defendants than to unattractive ones. Kampe et al. (2001) showed that reward circuits in the brain are activated when attractive people turn their gaze on oneself.

The benefits of attraction are shown to start early in life. Clifford and Walster (1973) studied the effect of physical attractiveness on teacher's expectations from their 5th grade pupils. They found that a child's attractiveness was predictive of the teacher's judgements of how intelligent the child was, how likely he or she was to pursue school, and how popular they would be amongst their peers. Perhaps more distressingly, Langlois et al. (1995) found that mothers of more attractive infants were more playful, affectionate, and attentive with their children compared to mothers of less attractive infants.

Why do we prefer attractive individuals? One explanation could be that we assume that attractive individuals also have nicer personalities. Dion et al. (1972) asked 30 male and 30 female undergraduate students to rate pictures of attractive and unattractive people on several personality traits. They found that attractive people were rated higher on friendliness, sociability, trustworthiness, and even on competence. The authors called this the "what is beautiful is what is good' stereotype.

Evolutionary social psychology provides an alternate, although not incompatible, explanation for why looks matter. Buss (1995) suggested that physical appearance might reflect good health and resourcefulness, and therefore might confer an adaptive advantage. Since these qualities might increase chances of procreation, people evolved to like people with good looks. However, this explanation is questioned, for instance by Weeden and Sabini (2005), who reviewed evidence from studies in Western societies and found a minimal relationship between attractiveness and physical health.

All in all, we have now looked at four factors that might lead to increased social affiliation: proximity, familiarity, similarity, and physical attractiveness. We now turn our attention to the neuroscience of social connection.

1.2 Neuroscience of social cognition

The Social Brain Hypothesis

Early studies in neuroscience assumed that brains evolved to solve ecological problems like foraging for food. However, they could not explain why the human brain took up around 2% of our total body weight and consumed around 20% of our energy intake (Dunbar, 1998). Therefore a puzzling question arose: why did primates, especially humans, evolved relatively larger and more energetically demanding brains compared to other species? To reconcile this discrepancy, Dunbar (1998) proposed the social brain hypothesis, which posited that large brains evolved to meet the computational demands of complex social behaviours like co-operation, competition, and deception. At first, this hypothesis came to be dubbed as the Machiavellian intelligence hypothesis, but later variants have often more simply been referred to as the 'social brain hypothesis'.

In support of the social brain hypothesis, several studies found a relationship between brain size and social group sizes. For example, Dunbar (1998) showed that neocortex size in anthropoid primate species correlated with social group size, but not so with ecological measures like percentage of fruit in the animal's diet. Sawaguchi and Kudo (1990) found that neocortex size was significantly larger for polygynous primate groups than their monogynous counterparts. Besides primates, neocortex size was also correlated with social network size in carnivores and insectivores, thus supporting the generalisability of the social brain hypothesis.

If brains evolved as an adaptation to handle complex social problems, then our ability perform social tasks must be constrained by our neocortex volumes. In the most basic form, this leads to the prediction that neocortex volumes would offer a constraint on how many stable social relationships we can maintain at any given time. Extrapolating the regression line between neocortex volume and mean group size for primates, the total number of relationships humans can stably maintain was found to be about 149 (Dunbar, 1993), a number popularly referred to as 'Dunbar's number'. Interestingly, this number was quite similar to the observed clan size of human hunter-gatherer societies.

While most primates show a strong correlation between neocortex size and group size, there are some notable exceptions. Consider, for example, the orangutan. Their relative neocortex size is close to that of chimpanzees, which should imply that they are found in large groups; yet, they seem to lead a semi-solitary life (Dunbar, 1993). Similarly, Hylobates, based on their neocortex sizes, are predicted to have group sizes of about 14. Yet, the observed sizes are around 5, nearly one-third of those predicted. These exceptions suggest that factors like the degree of a species' sexual dimorphism (differences in sexes of the same species) and implicit social bonds (bonds that go beyond the groups individual animals explicitly engage with) may play a role in determining their neocortex sizes.

Representation of the Self

In social situations, the brain must be able to effectively track oneself. Studies have shown that people remember more information when they are asked to relate it to themselves. This phenomenon is often termed the self-reference effect (Gazzaniga et al., 2019). For instance, Rogers et al. (1977) asked 59 undergraduates to rate various adjectives, and found that people were best able to recall adjectives when they were linked with oneself. This led the authors to conclude that the self is a unique cognitive construct which might be supported by its own distinct cognitive processing mechanism.

If the self is indeed a unique cognitive construct, then it must merit being represented by distinct brain regions or networks. Kelley et al. (2002) conducted one of the first neuro-imaging experiment to test this hypothesis. They recruited 24 participants and asked them to judge adjectives in one of three ways: self (e.g. "Does the adjective describe you?"), other (e.g. "Does the adjective describe the current U.S. president?"), or case-judgement (e.g. "Is the adjective presented in uppercase?). Like similar experiments, they found that participants reliably showed the self-reference effect. In other words, they found that people were more likely to remember words from the self-reference condition compared to the other conditions. Then, using fMRI, they found that the medial prefrontal cortex (MPFC) was differentially activated in the self-reference condition compared to the other conditions.

Our associations need not necessarily be with personality traits to trigger the self-reference effect; even associating shapes with oneself led people to be faster and more accurate than when associating shapes with others (Sui and Humphreys, 2015). People had better memory recall when objects were owned by oneself compared to others (Cunningham et al., 2008). Ownership bias was observed across multiple levels of behaviour, from initial preferences to reaction times to learning rates, with brain regions like the ventromedial prefrontal cortex and anterior cingulate sulcus (ACCs) showing stronger responses for self vs stranger associations (Lockwood et al., 2018). Murray et al. (2012) conducted a meta-analysis to understand the areas of the brain that distinguish between self, a close other, and a public figure. They found that activity in the dorsal and ventral parts of the anterior cingulate cortex (ACC) encoded self-specific activity in contrast to close others or public figures.

Interestingly, the self-reference effect is observed even when people are supposedly at "rest". Several studies have found that when participants had their eyes closed or were looking at a fixation cross, a network of brain regions which included the MPFC was active; when the researchers quizzed these participants about what they were thinking during rest periods, the typical answer was related to onself (Gazzaniga et al., 2019).

When we are at rest, blood continues to flow through various regions of the brain. Gusnard and Raichle (2001) reviewed several unrelated functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) studies, and found that neural activation at rest was not random, and engaged a similar network of brain regions as that involved in self-related processing. They suggested that this network could be a baseline, or default, network of brain function and labelled it the default mode network (Raichle et al., 2001).

The default mode network consists of brain regions like the dorsomedial prefrontal cortex (dmPFC), vmPFC, precuneus, posterior cingulate cortex, retrospenial cortex, temporo-parietal junction (TPJ), medial temporal lobe, and the inferior parietal lobule (Gazzaniga et al., 2019). The default mode network is most active during tasks involving self and inwardly focused attention, like engaging in self-reflective thinking or daydreaming. There are no primary sensory or motor regions involved in this network, which might suggest that one way to disengage from self-referential thinking is to do something active like practicing guitar chords or playing chess.

Theory of Mind

After the discovery of the default mode network, several studies found that a strikingly similar set of brain regions were activated when we think about the thoughts and beliefs of other people. For instance, Spunt et al. (2015) used fMRI to test for regions showing brain activation during and preceding three different cognitive tasks: judging whether a sentence represented the mental state of an individual, a physical description of an object, or solving an arithmetic problem. They found that the default mode network was active when participants actively judged beliefs about other individuals. Furthermore, they found that activity in the default mode network, particularly in the dmPFC, preceding the mental state judging task predicted the ease and efficiency of participants' performances during the task. On the other hand, default mode network activity preceding the physical description and math condition did not predict performance in the task.

The ability to ascribe mental states to oneself and to others is known as theory of mind (ToM) (Premack and Woodruff, 1978). There are two dominant theories about how we attribute mental states to others (Gazzaniga et al., 2019). The first, mental state attribution theory, suggests that we use information we know about other people, like happenings in their past, their body language, eye-contact etc., and infer their mental states by integrating this information. In other words, mental state attribution theory posits that we use cognitive information for inferring the mental states of others. Another alternative theory, simulation theory, posits that we simply observe other people's behaviour, simulate it in our minds, and then use the resulting mental state to infer the mental states of others. There is evidence to suggest that we could use both these routes in making theory of mind judgements.

Let's first examine evidence in favour of mental state attribution theory. Mitchell et al. (2005) provided participants written information about certain people along with a photo of their faces and asked them to judge the personality of the photographed individual (information formation task). For example, a given face could be accompanied by a written prompt which read: “At a party, he was the first to start dancing on the table”. For a control condition, the authors made participants remember the order in which the faces and information appeared (sequencing task). Both the information formation task and the sequencing task required people to think about other people, but only the former required them to infer internal states. In the impression forming task, the researchers found that the dmPFC was more active than in the control condition. They also found that the activation was specific to forming impressions of people, and forming impressions of inanimate objects did not equally activate the dmPFC.

Mental state attribution computations are not limited to the MPFC alone. Saxe and Baron-Cohen (2006) made participants read stories describing other people's thoughts, appearances, or bodily sensations. They found that regions—the right temporoparietal junction (rTPJ), left temporoparietal junction (lTPJ), and the posterior cingulate—were selectively active when participants read about other people's thoughts as opposed to other subjective states like bodily sensations or socially relevant information like their physical appearance. In another study, Saxe et al. (2009) found that the same regions were active when children aged 6–11 listened to sections of a story that described the character's thoughts. Interestingly, the rTPJ was active when younger children listened to mental and physical facts about other people, but only active when older children listened to mental but not physical facts about others. This suggests that the rTPJ develops selective theory of mind capabilities as part of our developmental process.

The second dominant theory suggests that we simulate other people's thoughts and behaviour in our minds and use the resulting mental state to form a theory of mind. Several researchers considered mirror neurons—neurons that activate in response to a given action irrespective whether performed by oneself or others—as the basis of simulation theory (Gazzaniga et al., 2019). In humans, several structures were activated during action observation and action execution, which is proposed as the human mirror neuron network. These brain areas included the rostral inferior parietal lobule, dorsal premotor cortex, MFC, and ACC.

Similar to how we simulate other people's actions, we may also simulate other people's feelings. In fact, we call this capacity to share others' feelings by a special name: empathy. Wicker et al. (2003) evoked strong feelings of disgust in participants by making them inhale an unpleasant odourant. Later, they showed the same participants videos of facial expressions of disgust. They found that both experienced disgust and observed disgust activated the same region in the brain, namely the anterior insular (aI) and to a lesser extent the ACC. The authors interpreted their findings as evidence for shared representation of emotions.

Along similar lines, Singer et al. (2004) found that the ACC and aI were activated when participants experienced pain, but surprisingly also when their romantic partners experienced pain. Participants in their study were administered a painful electrical stimulus or shown a cue on a computer screen which indicated whether their partner, who was also in the same room, was receiving the same painful stimulus. Using fMRI, they found that the aI and ACC were activated when participants experienced pain themselves or when they saw a signal indicating that their partners were experiencing pain. Further, they found that the ACC/aI activity correlated with their self-reported empathy scores.

In conjunction, these findings underline the importance of simulating others' thoughts and feelings, thereby reinforcing the importance of simulation in social cognition, including potentially also in ToM.

Amygdala and Social Emotions

Another region that is shown to be involved in inferring emotions of others is the amygdala. Studies have shown that the amygdala is involved in processing social stimuli, particularly those of an emotional nature (Gazzaniga et al., 2019). Adolphs (1994) showed that a patient, S.M., with selective damage to their amygdala, had no trouble identifying faces, but had trouble recognising the expression of fear on faces.

Successful social communication requires the ability to both receive and send emotional signals. Anderson and Phelps (2000) studied a person with bilateral amygdala damage and found that the deficits appear to affect only the interpretation of facial expressions of emotions, including fear, but not the expression or acting out of these emotions. This finding suggested that the amygdala, or any single part of the brain, is not responsible for undertaking all aspects of social communication.

The amygdala appears to be involved in the recognition of emotional expressions in general, and not just those of fear. For example, Breiter et al. (1996) scanned healthy participants using fMRI while they were presented with fearful, happy, and neutral faces. They found that the amygdala was significantly more activated when participants saw fearful faces compared to neutral faces. When the order of stimuli presentation was counter-balanced, the amygdala was also active when participants saw happy faces versus neutral faces. Morris et al. (1998) used positive emission tomography (PET) to scan participants as they saw happy and fearful faces and found that the amygdala was significantly more activated when participants saw fearful faces compared to happy ones. In a meta-analysis of 105 studies, Fusar-Poli et al. (2009) found that happy, fearful, and sad faces specifically activated the amygdala, with fearful faces showing the stronger response compared to happy or sad ones. This suggests that the amygdala may have a role to play in encoding emotional valence in general, but may have evolved to be especially sensitive to the emotion of fear.

About a decade after testing S.M., Adolphs et al. (2005) proposed a mechanism to explain S.M.'s inability to recognise fearful expressions. Using computer software to selectively hide different parts of the face, the researchers discovered that S.M.'s impairment stemmed from an inability to utilise the eye region when judging emotions. In other words, while people without amygdala damage inferred emotions by fixating on the region including and surrounding the eyes, S.M. did not show any special preference to fixate on this region. Furthermore, when S.M. was explicitly asked to look at the eyes, her recognition of fearful expressions returned to normal.

The role of the amygdala is not restricted to the evaluation of facial expressions. Damage to the amygdala also seems to affect whether or not animals affiliate with others in their social world. For example, Mirsky (1960) suggested that monkeys with lesions to the amygdala were less fearful toward the experimenters, and rose from bottom to top in social rank amongst their social group. Aspiration lesions to the anterior temporal cortex, including the amygdala, was shown to result in complete social isolation in rhesus monkeys (Bachevalier, 2000).

An analogous decrease in affiliative behaviour following amygdala damage is less common in humans. However, patients with anterior temporal lobectomy displayed fewer social interactions and increased antisocial behaviour (Bachevalier, 2000). Tranel and Hyman (1990) described a patient having bilateral calcification in their amygdala who displayed irrational and inappropriate social behaviour. Adolphs et al. (1998) asked three patients with bilateral amygdala damage to judge faces on their trustworthiness and approachability. They found that all three subjects found faces of unfamiliar individuals more approachable and more trustworthy than did control subjects.

While historically the amygdala was viewed as a 'threat detection device' or a 'fear module', recent studies point at its role in encoding positive affect (Murray, 2007). Paton et al. (2006) recorded activity from the amygdala in monkeys while they learned to associate neutral stimuli with positive or negative reinforcements. Monkeys in their experiment saw abstract pictures which were paired with either juice (positive reward), a puff of air (negative reward), or nothing (no reinforcement). They found that distinct populations of neurons in the amygdala coded for both positively and negatively valenced reinforcers. In humans, Somerville et al. (2006)

showed participants unfamiliar faces along with information which was either positive or negative in valence (eg. “Emily helps the homeless”, or “Bob is a deadbeat dad”). They found that the right amygdala was activated in trials with positive and negative valence, suggesting that the amygdala might represent general emotional valence and not specifically negative valence.

Recent work has shown that the amygdala might also be involved in social decision making. Grabenhorst et al. (2019) recorded amygdala neurons from macaque monkeys as they performed a reward-based learning task. Each monkey was partnered with another monkey, and they both alternated between doing the task themselves and observing their partner doing the same task. The researchers found that amygdala neurons encoded object values not just when a monkey performed the task, but also when they observed a partner monkey doing so. These values were used by monkeys to make their own choices, but another set of neurons showed a similar pattern of activity before their partner’s choices — as if these neurons were simulating their partner’s decision.

All in all, the amygdala plays a key role in social cognition, including recognising emotional valence in facial expressions and representing decision variables for self and others.

Social Rewards

Social situations are inherently rewarding, and several studies show such rewards might be encoded in the striatum. The striatum is part of the basal ganglia, a neuronal circuit responsible for initiating and controlling movements (Báez-Mendoza et al., 2013). It comprises three nuclei: caudate, putamen, and the ventral striatum. The striatum shows neural activity related to movement, reward, learning, and their conjunction. It also shows activity in response to expectations and prediction errors (the differences between expectations and outcomes) when receiving rewards (Schultz et al., 1997). The striatum receives input from subcortical structures like the substantia nigra pars compacta and the amygdala, and also from the medial prefrontal cortex, where social and reward information is processed (Noritake et al., 2021). In turn, it projects to the substantia nigra pars reticulata and the globus pallidus, which are the two main output nuclei of the basal ganglia.

The striatum has been shown to be involved in representing social reward. For example, donating to charity resulted in good feelings—the so called 'warm glow'—and elicited activity in the areas associated with reward in the brain, including the striatum (Harbaugh et al., 2007). Interestingly, the mere act of observing someone we like receive reward is rewarding in itself. For instance, Mobbs et al. (2009) asked their participants to watch films portraying two confederates who expressed themselves in a socially desirable or undesirable manner. This led to the participants liking one confederate and disliking the other. Next, participants were scanned using fMRI as they watched films of these confederates playing a game and receiving rewards. The authors found that participants found it more rewarding to see the socially desirable confederate win than the undesirable one. Further, the authors found that desirable confederates were more likely to elicit a stronger increase in ventral striatum activity than did the undesirable confederates. The authors suggested that vicarious rewards might explain why we find game shows exciting and enjoyable to watch.

In several social situations, we receive reward from someone else's actions (Báez-Mendoza et al., 2013). For example, touch is often considered to be pleasant, especially when received in infancy and in childhood from caregivers (Cascio et al., 2019). Similarly, receiving praise from others can also be rewarding, and such rewards are found to be represented in the ventral striatum (Korn et al., 2012). Acquiring a good social reputation is often an incentive in human actions. Izuma et al. (2008) scanned participants using fMRI as they played a social decision-making task in which the reward was an increase in social reputation. They found that an acquisition of reputation robustly activated reward-related areas and most notably the striatum.

Just like in humans, the striatum also plays an important role in representing social action and social reward in primates. Báez-Mendoza and Schultz (2013) tested two monkeys as they sat across from each other and pressed a button to either receive rewards in four conditions: reward for neither, own reward only, conspecific reward only, reward for both. They found that striatal neurons coded mainly for own reward, but also occasionally for conspecific's reward. Other striatal neuron encoded when the reward was delivered from a conspecific's action, an effect that was mitigated when the actions were simulated by a computer, suggesting a social rather than observational role of the striatum. Further, Báez-Mendoza et al. (2016) found that striatal neurons in macaques encoded reward inequity: the difference between one's own reward and other's reward. Two monkeys sat across from each other and received rewards which were distributed either equally or unequally. The researchers found that a group of neurons in the striatum encoded reward inequity, irrespective of whether inequity was advantageous or disadvantageous. This result suggests that striatal neurons keep track of the difference between one's own reward and other's rewards.

Apart from the striatum, the ACC also seems to have a role in representing social reward. For example, Korn et al. (2012) found that the reward from social praise was encoded in the striatum as well as the ACC. Social pain, for instance, that which arises from social exclusion, is also represented in the ACC. Eisenberger et al. (2003) scanned participants as they played a ball tossing game (called "CyberBall") with other fictional players. During the game, the players tossed the ball between themselves, but after a certain point the computerised players excluded the participant from the game. The researchers found that the ACC was more activated during social exclusion than during inclusion, and its activity correlated with self-reported distress. Given that the ACC was shown to respond to physical pain, Eisenberger (2012) suggested that social pain and physical pain might have a shared representation in the ACC.

Basile et al. (2020) showed that lesioning the ACC prevented macaque monkeys from learning what actions bring reward to others (prosocial actions). Remarkably, removal of the ACC did not stop the monkeys from carrying out previously learned prosocial actions. Indeed, learning what actions reward others might be supported by a separate neural mechanism than undertaking such actions (Lockwood and Klein-Flügge, 2020). A specific sub-region of the ACC, in the gyrus (ACCg), has been showed to be particularly important for social information processing. Apps et al. (2016) suggested that computational properties of the ACC support social cognition by estimating the motivation levels of other individuals, and further updating those estimates when evidence when found erroneous.

All in all, social reward seems to be represented in the striatum, but also in some other parts of the brain like the ACC.

Social Context

In this section, I will examine the brain regions that represent features of our social environment. Humans spend a large amount of time navigating social environments, and the most dorsal part of the medial prefrontal cortex—the dorsomedial prefrontal cortex—may be encoding key features of one's social environment (Klein-Flügge et al., 2022a).

One aspect of the social environment that is studied extensively is whether an environment is co-operative or competitive. Competitive and co-operative environments have a key impact on an individual's or animal's fitness, health, and longevity. For instance, Schülke et al. (2010) found that female macaques who co-operated more lived longer and had higher offspring survival, whereas co-operative male macaques had higher number of offsprings. In humans, as discussed earlier, loneliness is linked to higher mortality risk and adverse health outcomes (see section on social ties and well-being[2])

Wittmann et al. (2016) have found that our estimate of our own performance changed based on whether we are co-operating or competing with others. Participants in their study played a series of games and were told about their performance in these games. Simultaneously, they were also informed about the performance of other

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[2] social-ties-and-physical-well-being

pre-programmed “players”. On some trials, participants were placed in a co-operative frame with other players (the sum of their performances determined their payoff) whereas in other trials they were put in a competitive frame (the difference in their performance determined the payoff). The authors found that participants’ assessment of their own performance was influenced by others’ performances, a phenomenon they called ‘self-other mergence’. They found that in a collaborative frame, people rated their own performance as stronger when they were paired with stronger players. On the contrary, in a competitive frame, people rated their own performance as weaker when they were paired with a stronger player. Further, they found that the dmPFC tracked the contextual effect of one’s own performance on one’s estimation of others’ performance.

In monkeys, dmPFC activity is also shown to represent values of reward for oneself and others. Noritake et al. (2018) seated two macaque monkeys in front of a display screen and conditioned them with an abstract stimulus that preceded liquid reward. The animals were studied in two contexts: a self-variable context, in which the probability of reward for the monkey studied (referred to as ‘M1’) changed based on the different stimuli but remained constant for the other monkey, and another variable context, in which the probability of reward changed for the other monkey and remained the same for M1. As expected, the authors found that M1’s anticipatory licking behaviour increased with increasing reward probability in the self-variable block. Interestingly though, they found that M1’s anticipatory licking behaviour decreased as partner reward probability increased, even though M1 was rewarded equally often regardless of partner reward. This finding suggests that macaques might attribute lower value to their own reward when partners are rewarded more. This is consistent with the finding discussed in the previous section, where Báez-Mendoza and Schultz (2013) found that the attractiveness of rewards were linked with not just the absolute value of one’s own reward but rather its relative value to other animal’s reward.

Noritake et al. (2018) recorded single neurons from the MPFC and found that a subset of neurons, which they labelled 'self-type neurons', increased their activity with increasing self-reward probability. In other-variable contexts, these neurons showed a constant response indicating that computations in the MPFC happen prior to subjective value computations. On the other hand, a distinct subset of 'partner-type neurons' increased activity with increasing probability of partner's reward. These signals were later integrated into a subjective utility signal, which the authors found to be represented in the dopaminergic midbrain. In a recent review, Noritake et al. (2021) suggested that subcortical areas like the amygdala, lateral hypothalamus, and striatum may also help animals integrate social contexts into a utility signal which helped with making social decisions.

Like the dmPFC, the orbitofrontal cortex (OFC) might also play a role in keeping track of various social contexts. Humans are faced with a variety of social contexts that come with unspoken rules. For instance, handshake etiquettes vary from country to country (Gazzaniga et al., 2019). Similarly in the west, hugging someone you know might be normal, but hugging a stranger might be socially inappropriate. How are these features and rules of the context tracked by the brain? Certain studies suggest that the OFC might have a role to play.

In one study, Stone et al. (1998) presented participants with scenarios in which a character says something impolite, and therefore violates rules of the social context. In one scenario, Anne receives a flower vase as a gift from Jeanette. A year later, Anne forgets about the gift. One day, Jeanette visits Anne and accidentally breaks the flower vase. Anne tells Jeanette not to worry, because it was a wedding gift she never liked anyway. The researchers asked participants to identify if anyone in such scenarios had made a social mistake and why.

The researchers found that given such a scenario, patients with OFC damage did not perform as well as healthy control or patients with lateral prefrontal damage (Stone et al., 1998). These patients had a hard time understanding that Anne's comment was intended to reassure Jeanette, and they instead believed that Anne intended to hurt Jeanette's feelings. In other words, the patients were not able to take the context of friendship into account while reasoning about social situations.

In another study, Beer et al. (2003) tested patients with OFC damage in a task where participants had to make up nicknames for a stranger. The researchers found that people with OFC damage offered unflattering nicknames and delivered them in a singsong tone, a type of behaviour usually reserved for someone we know well. Moreover, the OFC lesioned patients were not embarrassed by their behaviour, and some even reported being proud of it. Taken together, these studies suggest that the OFC may have a role to play in assessing social context.

1.3 Behavioural and neural representations of social environments

Theoretical accounts of the role of environments in decision making

Having surveyed general themes in social neuroscience, we now turn our attention to the specific question of how social contexts might affect social decisions, and which brain regions might be involved in representing such decisions. Research in social neuroscience has been fruitful in probing underlying neural mechanisms, but little attention has been paid to how experimental tasks relate to real world social decisions (Gabay and Apps, 2021; Mobbs et al., 2018). This discrepancy between experimental tasks and real world problem has led to the argument that fields like behavioural ecology could lead to more naturalistic hypotheses about social environments (Gabay and Apps, 2021).

To account for the role of background environments in social affiliation decisions, we will consider three theoretical accounts that will help inform hypotheses about social decisions: (a) behavioural ecological theories on how an animal behaves in various foraging environments, (b) studies on macaque monkeys exploring the role of the dorsal raphe nucleus (DRN) in representing background environments, and (c) theoretical models of rat free-operant behaviour in environments with different reward rates.

Studies from behavioural ecology show that an animal's environment plays a role in shaping decisions, above and beyond the object of reward they seek. If social reward is considered analogous to dietary reward, then social environments might also play a role in influencing social decisions. Aspects of our social behavior, such as our choice of friends, suggest that fundamental features of our environment, even those of which we are only dimly aware, play an important role.

The suggestion that the environment would play a role in social decisions builds on ideas from behavioural ecological studies of animal foraging. To study how a predator forages in an environment with patchy rewards, Krebs et al. (1977) placed hungry titmice (a small European bird in the same family, Paridae, as the chickadees) in a cage which overlooked a conveyer belt through a hole in its floor. The experimenters placed two types of mealworms on the conveyer belt. The bird had to decide which types of mealworms to eat and which to ignore. The decision was based on three factors: the types of worms, how frequently both types of prey were encountered, and the effort required to capture and eat these worms.

Krebs et al. (1977) found that when the encounter rate with both types of prey was low, the birds were non-selective between the types of prey they ate. But when the encounter rate was high, the birds selectively ignored the less profitable type and did so irrespective of the encounter rate with them. If humans are guided by a similar process to select their social affiliates, I would expect people to be more selective in initiating social connections in denser environments which would offer greater social opportunities.

In their review of foraging theories, Pyke et al. (1977) described an optimal model of foraging that birds use to increase their net rate of energy intake. According to their model, when exploiting different patches of land for prey, birds chose to allocate more of their resources to an abundant environment when compared to a less abundant environment. For the purposes of social decision making, this result would suggest that we would be more likely to initiate social affiliation in friendlier and more affable environments.

While classical foraging theory concerns itself with how animals forage for food, studies from social foraging theory account for foraging behaviour in the presence of other conspecifics (Giraldeau and Dubois, 2008). Such "social foraging" models argue that when animals forage in groups, the resource allocation between themselves also plays a factor in their decisions to choose the appropriate patches and prey types.

On the neural level, a series of studies have shown that background environments influences choices in macaque monkeys. For instance, Wittmann et al. (2020) showed that macaque monkeys maintained an estimate of the global reward state and that this reward trace influenced their decisions. Wittmann et al. (2020) found that the average reward rate influenced choices and was represented in the DRN and aI of macaque monkeys. Further, the dmPFC area 9 also responded to social contexts. Priestley et al. (2024) showed that the DRN activity patterns change when transitioning from rich environments with abundant rewards to poor environments with scarce rewards. Further, non-invasively disrupting DRN activity using transcranial ultrasound stimulation diminished sensitivity to environmental richness so that animals made fewer adjustments to their behaviour as the background changed.

In humans, Trier et al. (2023a) showed that in a virtual naturalistic environment, people freely switch between foraging for reward and being vigilant for threat, and both these behaviours were tracked in a network spanning the DRN, the lateral habenula, ACC, and aI. Further, individual variation in vigilance was correlated with activity in the DRN. Given that the DRN is a major source of serotonin in the brain, it is possible that a serotonergic system involving the DRN, and its anatomical connections to the hypothalamus, habenula, dmPFC, and aI, might be involved in representing environmental contexts.

Another set of regions that might be involved in tracking environmental context are those in the dopaminergic midbrain. Niv et al. (2007) suggested that tonic dopamine neurons in the substantia nigra (SN) and ventral tegmental area (VTA) play a key role in encoding opportunity cost in rat foraging behaviour. When the average rate of reward is high, there is a higher opportunity cost to not acting. In such circumstances, Niv et al. (2007) argued that rats should exert more effort to harvest more reward while it is available and abundant. When the average rate of reward is low, however, there is a lesser opportunity cost to not acting and therefore Niv and colleagues argued that rats should exert less effort; it is not worth responding vigorously to harvest new rewards because new opportunities were now less likely to be encountered. The authors suggested that this average rate of reward, and the opportunity costs that they afford, is tracked by tonic dopamine in midbrain neurons.

Gabay et al. (2024) reported an analogous opportunity-cost sensitive behaviour when humans made decisions to stay or leave the company of others who made economic offers with varying degree of fairness, in social environments with different opportunity costs. Across four studies, Gabay et al. (2024) found that people leave others when the opportunity costs are high, indexed by average fairness of the environment and the effort required to connect to another partner. Further, people's leaving times were linked to their depression and loneliness scores, suggesting mental health dimensions might explain our social decisions, a link I will test in chapter 3. Vogel et al. (2024) showed that prosocial decisions to help others might also be linked to the opportunity costs of environments; the researchers showed that people were more inclined to interrupt their behaviour to help others in poor environments compared to rich ones.

Using analogies from the theoretical accounts involving foraging environments, we hypothesised that a serotonergic and dopaminergic system might be involved in tracking social environments in our studies. In particular, we selected the following areas as a priori regions of interest: the DRN hypothalamus, habenula, SN, VTA, dmPFC, and aI. I will now describe what is known about the structure and function of these regions of interest in more detail.

Dorsal Raphe Nucleus

The DRN is located in the brainstem beneath the midbrain aqueduct, and is the source of most serotonin neurons projecting throughout the brain (Beliveau et al., 2015). There are about 9000 serotonin neurons in the mouse DRN (Ishimura et al., 1988), and about 160,000 serotonin neurons in the human DRN (Baker et al., 1991).

DRN neurons send ascending projections to various midbrain and forebrain areas that are implicated in reward processing, emotional control, and sensorimotor integration (Liu et al., 2020). These areas include the dopaminergic substantia nigra pars compacta (SN)/ventral tegmental area (VTA), hypothalamus, and the insular and frontal cortices (Vertes, 1991). There is also evidence for projections from the DRN to the amygdala, thalamus, and the olfactory bulb.

Similarly, areas involved in emotional regulation, reward processing, and decision making send projections to the DRN. The DRN receives such serotonin projections from areas including the prefrontal cortex, lateral habenula, hypothalamus, VTA, and more (Ogawa et al., 2014; Pollak Dorocic et al., 2014). While the DRN is often associated with serotonin neurons, it is worth noting that serotonin neurons make up for less than half of the total cells in the DRN, and that they are mixed with GABA, glutamate, and dopamine neurons (Fu et al., 2010; Liu et al., 2020).

While the role of DRN in tracking background reward is not well understood, its role in processing foreground reward is more widely studied. Inaba et al. (2013) showed that primate DRN responds to all features of a reward-based task like initiation, expectation, and the sign and value of the actual outcome. They further showed that neuronal activity increased as the task progressed toward reward, suggesting a tonic release of serotonin in maintaining states of the task. In contrast, using fibre photometry, Li et al. (2016) showed that rewards like food, sex, and social interaction activated DRN neurons in a phasic manner, but aversive stimuli like foot-shocks did not. This suggests that DRN neurons release serotonin both in a phasic and tonic fashion to process rewards.

Doya and colleagues showed a waiting effect in serotonin neurons. They found that serotonin neurons in the DRN tonically increased their firing rates when rats waited for food or water rewards (Miyazaki et al., 2011). Further, inhibition of DRN activity using a serotonin receptor agonist sertraline impaired rats' tolerance for delayed rewards (Miyazaki et al., 2012). These results suggest that the DRN serotonin activity is necessary for our ability to delay gratification.

Serotonin has been linked to the experience of pleasure (hedonia) and subsequently to psychiatric states like depression. Humans report a feeling of euphoria when consuming drugs like MDMA that target serotonin neurons (Liu et al., 2020). By contrast, nicotine produces lesser pleasure and is shown to have a lower impact on serotonin tone, despite strongly activating dopaminergic neurons. Despite the emphasis on dopamine as the pleasure and reward molecule, dopamine deprived mice have been shown to have preferences for sucrose over water, including the sweetener saccharin (Cannon and Palmiter, 2003), and drugs like morphine (Hnasko et al., 2005). However, there is no direct evidence that these residual preferences are explained by serotonin or the DRN alone. All in all, the link between serotonin and depression is not without its debate. I will discuss whether a lack of serotonin activity is the basis of depression, the so-called "serotonin hypothesis of depression" in the section on major depression.[3].

The specific role of the DRN in social interactions is relatively unexplored. Li et al. (2021) showed that DRN to ACC connectivity modulated consolation and sociability in mandarin voles. They found that chemogenetic or optogenetic inhibition of serotonin neurons in DRN or optogenetic inhibition of serotonin terminals in the ACC decreased the animals' grooming, sniffing, and approaching behaviour. They also found that activation of serotonin receptors in the ACC was sufficient to reverse some of these social deficits that result from an inhibition of the DRN serotonin neurons.

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[3] depression-and-affective-disorders

Hypothalamus

The hypothalamus ("hypo" meaning below, and "thalamus" meaning bed) is a small pea-sized region constituting less than 2% of total brain volume (Fong et al., 2023). It is most well-known for containing neural circuitry that supports basic life functions like energy metabolism, digestion, and thermoregulation (Saper and Lowell, 2014). It receives a range of sensory inputs and integrates these signals to support life processes through behavioural, autonomic, and endocrine pathways (Fong et al., 2023). It is divided symmetrically across both hemispheres of the brain, with the third ventricle delineating the two sides.

The hypothalamus is made up of several nuclei, most often classified along the rostral-caudal axis using post-mortem and neuroimaging methods (Fong et al., 2023; Jensen et al., 2024). The rostral part, also called the pre-optic area, lies above the optic chiasm and comprises nuclei such as ventrolateral pre-optic nuclei, the medial and lateral pre-optic areas, and the suprachiasmatic nucleus (Fong et al., 2023; Saper and Lowell, 2014). These regions, especially the suprachiasmatic nucleus, play a crucial role in regulating our circadian rhythm. The middle part, also known as the tuberal hypothalamus, includes the lateral and anterior hypothalamic areas, and comprise the dorsomedial, ventromedial, paraventricular, supraoptic, and arcuate nuclei. This part contains inputs for functions like feeding and outputs for functions like sexual behaviour and aggression. Finally, the posterior hypothalamus includes mammillary bodies and the posterior hypothalamic nuclei. This region provides output to regions regulating arousal and wakefulness.

All in all, the hypothalamus serves as an integrative region which brings together a wide range of sensory inputs and those important to support basic life functions (Saper and Lowell, 2014). It then uses set-points to determine ideal levels for bodily parameters such as temperature, hormone levels, wakefulness and more. It directly innervates the parasympathetic and sympathetic neurons, as well as nuclei in the brain stem that control autonomic responses. In a large scale study using resting state fMRI data (n=498), Jensen et al. (2024) showed that the functional connectivity of hypothalamic nuclei with other brain regions can predict dimensional markers of stress in humans.

From a social perspective, the hypothalamus plays a role in regulating sexual, parental, and agressive behaviours (Mei et al., 2023). The key regions implicated in social behaviour include the medial preoptic nucleus, ventromedial hypothalamus, and the ventral premammilary nuclues. This set of regions is dubbed the reproductive behaviour control column (RBCC). Further, Fan et al. (2023) showed that experimentally induced loss of social status in mice resulted in the activation of the lateral hypothalamus-lateral habenula circuit.

Habenula

The habenula (Hb) is a pea sized region that is conserved across vertebrates (Namboodiri et al., 2016). It is part of the epithalamus, along with the pineal gland, and is surrounded by the thalamus. In mammals, it is split into two regions: the lateral and the medial habenula (Hikosaka, 2010).

Lateral Hb neurons project to areas involved in the production of serotonin, like the DRN (Hikosaka, 2010). They also project to dopaminergic areas like the substantia nigra and ventral tegmental area (SN/VTA). The medial Hb projects to interpeduncular nucleus, which further projects to medial and dorsal raphe nuclei, amongst other areas. Hence, it is thought that both the lateral and medial Hb regulate the release of both serotonin and dopamine in the brain.

The Hb receives input from cortical regions like the medial prefrontal cortex and the basal forebrain (Namboodiri et al., 2016). It also receives input from the hypothalamus, and indeed in the previous section, I described how social status loss might involve the habenula-hypothalamus circuit.

The neural network described above suggests that the Hb might play a key role in emotion-related behaviours (Hikosaka, 2010). Indeed, lesions of the Hb lead to disruptions in sleep, pain, stress, and reward-related behaviours. In sleep, the Hb seems to play a key role in regulating rapid eye movement (REM) sleep. Valjakka et al. (1998) lesioned the fasciculus retroflexus in rodents, a key fibre bundle with outputs from the Hb, and found that it reduced time spent in REM sleep by 79%.

Another study showed that animals with Hb lesions show decreased performance in a reaction time task (Lecourtier and Kelly, 2007), and this effect was believed to be modulated through the habenular connections to the dopaminergic system regulating movement. Indeed, Christoph et al. (1986) showed that stimulating the Hb in rats led to an inhibition of the dopamine neurons in the SN/VTA. On the other hand, Nishikawa et al. (1986) showed that habenular lesions increased dopamine concentrations in the medial prefrontal cortex and the nucleus accumbens.

The lateral habenula (LHb) plays a key role in many aspects of reward-based decision making. It is involved in reward processing, signalling negative prediction errors, and abstract inference, amongst other functions (Namboodiri et al., 2016). In reward processing, the LHb has often been called an "anti-reward centre" (Fan et al., 2023). This is because the LHb tends to be activated by a number of aversive stimuli. For instance, in an fMRI study, Ullsperger and von Cramon (2003) showed that negative feedback led to the activation of the habenula (in addition to the anterior insula and the anterior cingulate cortex). Lawson et al. (2014) observed positive Hb responses to cues signalling painful electric shocks. Using single cell recordings, Matsumoto and Hikosaka (2007) showed that macaque monkeys showed increased LHb activity when presented with a no-reward predicting target, and decreased activity when presented with a reward predicting target. In contrast, dopaminergic neurons showed the opposite pattern: excitation in response to reward, and inhibition in response to no-reward.

Failure to receive a reward can be disappointing, but to be punished is even more disturbing. Dafny and Qiao (1990) subjected rats to painful stimuli and found that it activated the Hb. Further, stimulation of the DRN neurons led to a decrease in firing rates of animals when subjected to painful stimuli. Amat et al. (2001) lesioned the Hb and found that it reduced the concentration of serotonin levels in the DRN.

Corroborating the findings from animal models, the Hb is shown to be involved in psychiatric illnesses like depression. Using positron emission tomography, Morris et al. (1999) showed that depleting tryptophan, a precursor to serotonin, resulted in a higher covariation of activity between the DRN and Hb in depressed individuals versus non-depressed individuals, and this activity correlated negatively with self-reported mood ratings. Similarly using resting state fMRI, Roiser et al. (2009) showed that acute tryptophan depletion led to increased blood flow in the Hb relative to controls.

A major symptom of depression is a lack of motivation and a reduced drive to move. Animals models of depression often use motor suppression to assess depression (Hikosaka, 2010). Both reduced motivation and motor suppression are attributed to hypo-activity in the dopamine system. Given the inhibitory effect of the Hb on dopamine neurons, it is possible that LHb activity predisposes an individual to depression-like states through its projections to midbrain dopaminergic areas like SN/VTA. These data suggest that the Hb may play a key role in regulating symptoms of major depressive disorder, and is a potential target for treatments using Deep Brain Stimulation (DBS).

In fact, Sartorius et al. (2010) reported a case of a 64-year-old patient who suffered from major depressive symptoms from her late teenage years. At the age of 55, she had her first severe depressive episode which included psychotic features. The patient was resistant to pharmacological treatment, including antidepressants and antipsychotic medications. Electroconvulsive therapy did not improve her condition much either. With multiple suicidal attempts and deteriorating quality of life, DBS was recommended.

The DBS procedure led to a full and sustained remission of depression symptoms (Sartorius et al., 2010). This effect was not immediate; the interval to remission was approximately 4 months. This delay, the authors argued, was convergent with DBS related effects at other stimulation sites, and might indicate that neural plasticity was induced in mood-related circuits. Using PET, the authors found increased metabolic activity in the LHb. Ever since this finding was first reported more than a decade ago, several other cases of remission following a DBS procedure targeting the Hb have been reported. However, larger control studies may be warranted before definite conclusions can be drawn about efficacy (Zhang et al., 2022).

Substantia Nigra/Ventral Tegemental Area

The substantia nigra (SN) and ventral tegmental area (VTA) are located in the midbrain and are the main producers of dopamine in the brain. Midbrain dopaminergic neurons in the SN and VTA regulate important motor and cognitive functions like voluntary movement, motivation, and learning (Luo et al., 2015). Dopaminergic neurons from the SN project to dorsal striatum through the nigrostriatal pathway. On the other hand, dopaminergic neurons from VTA project to the nucleus accumbens in the limbic systems via the mesolimbic pathway, and to the prefrontal cortex via the mesocortical pathway.

The neurons in the nigrostriatal pathways are believed to modulate movement through medium spiny neurons expressing D1 and D2 receptors (Luo et al., 2015). Indeed, movement-related symptoms in Parkinson's disease are thought to be caused by a loss of dopamine neurons in the SN. In addition to their role in movement, the neurons of the nigrostriatal pathway have also been shown to be involved in goal-directed behaviour and habit formation (Redgrave et al., 2010).

The neurons in the mesolimbic pathways have been proposed to support cognitive functions like motivation, learning, and reward processing (Luo et al., 2015). They are largely studied for their role in reinforcement learning, a term indicating the consolidation of stimulus associations with actions that lead to reward (Wise, 2004). Wise and Schwartz (1981) administered pimozide, a drug causing dopamine depletion, to hungry rats and observed a progressive decline in lever pressing behaviour to obtain food. Animals that were trained to obtain rewards initially continued their reward seeking behaviour following dopamine depletion, but eventually stopped it over the course of trials. Further, the decline in reward seeking behaviour was faster in a dopamine deprived state than in a state in which lever presses were no longer rewarded (Wise, 2004).

Rewards normally come with feelings of pleasure or elation. One hypothesis of dopamine function, the anhedonia hypothesis, suggests that dopamine plays a key role in mediating this pleasure. The evidence in favour of this hypothesis comes from studies that showed amphetamine induced euphoria correlated with dopamine release (Laruelle et al., 1995). However, overall, the evidence is weak, and we have seen in the section on serotonin/DRN that dopamine deprived animals continue responding to rewarding food items.

Berridge and Robinson (1998) distinguished between the ‘wanting’ and ‘liking’ of reward, and suggested that dopamine plays a role in the former but not the latter. They argued that dopamine enabled wanting behaviours like appetite, hunger, sexual drive, and not the subjective experience of pleasure. Another hypothesis suggested that dopamine is responsible not for encoding reward, but for encoding reward prediction (Schultz, 1998). In a seminal study, Schultz (1998) showed increased dopamine-neuron activations when animals expected to receive reward, and decreased activations when the expected rewards were not received. Further, the animals also responded to unexpected rewards, even when it was not associated with a cue. These results led to the idea that dopamine neurons encoded reward prediction errors, or more colloquially, a pleasant surprise.

Dopamine neurons operate in two modes: phasic and tonic (Grace, 1991). In their tonic mode, dopamine neurons release a baseline level of dopamine and changes in these levels are slow and steady (Bromberg-Martin et al., 2010). In their phasic mode, dopamine neurons sharply increase or decrease the release of dopamine in the span of 100–500ms (Schultz, 2007). For instance, the studies of reinforcement learning and prediction errors discussed above are thought to engage the phasic function of dopamine release.

Finally, dopamine is thought to play a role in multiple psychiatric conditions. We already discussed the role of dopamine neurons in Parkinson’s disease. While loss of dopamine neurons causes Parkinson’s, L-DOPA (a precursor to dopamine) is used in its treatment (Iversen and Iversen, 2007). Dopamine also seems to be involved in schizophrenia. The main line of treatment for schizophrenia, a class of drugs called antipsychotics, are thought to work by blocking dopamine receptors in the brain. Further, owing to its reinforcing effects, dopamine has been thought to play a role in addiction (Di Chiara, 2002). Finally, recent years have seen a rise in the diagnosis of attention deficit hyperactivity disorder (ADHD), and an inhibitor of dopamine transporter, methyl phenidate (more commonly known by its retail name Ritalin), is used to treat its symptoms. All in all, many psychiatric illnesses are associated with an abberation in dopamine-related neural processes.

Insula

The human insular cortex is a portion of the cerebral cortex folded deep inside the lateral sulcus. It is more than a single area and comprises a large region of cortex that has been linked to many functions, but the degree to which there is functional specialisation within it is unclear (Craig, 2009). It is a region of the human brain that has undergone the greatest relative expansion compared to other apes (Bauernfeind et al., 2013). The insula is a versatile region supporting many functions ranging from decision making, to interoceptive awareness, to representing subjective feelings of disgust and pain.

The insula is one of the most activated regions in human neuroimaging studies, yet it still remains poorly understood (Menon et al., 2020). This is partly thought to be due to its inaccessible location in the depths of the Sylvian fissure. Penfield and Faulk (1955) were able to access the insula of a patient who underwent lobotomy to relieve epilepsy, which as a result, exposed the insula. They observed that stimulation of the insula led to a variety of sensory responses in the face, tongue, and the upper limbs. Hence, one early hypothesis was that the insula was a dedicated region that supported visceral-somatic function.

The insula can be roughly divided into posterior and anterior regions. The posterior regions are the granular regions, and receive sensory inputs from the spinal cord, brainstem via the thalamus, in addition to inputs from the parietal and occipital cortices (Namkung et al., 2017). The anterior regions are the agranular regions and have reciprocal connections to the ventromedial prefrontal cortex, the amygdala, and the ventral striatum, amongst others. The anterior regions are frequently co-activated with the ACC, and the connection is considered analogous to that between the sensory and motor areas. Notably, the anterior insula contains high concentrations of spindle shaped neurons among the pyramidal neurons in layer 5 called von Economo neurons, which have a similar structural architecture to neurons in the ACC.

The numerous sensory features of the insula are broadly grouped under the umbrella term 'interoception' (Namkung et al., 2017). Interoceptive stimuli leading to insular activation involve thirst, hunger, dyspnea, 'air hunger', sexual arousal, warmth, exercise, and more (Craig, 2009). Craig et al. (2000) undertook a positron emission tomography study and showed that cool temperatures were represented in the dorsal posterior insula, whereas subjective ratings of these stimuli were reflected in the anterior insula. Therefore, a posterior-to-anterior mapping is often proposed, where the posterior regions are involved in representing primary sensory features, whereas the anterior regions represent secondary evaluations of such primary features. As a result, subjective feelings are thought to be represented in the anterior insula. Indeed, several recent imaging studies show that the anterior insula is activated in subjects experiencing emotional feelings, including maternal and romantic love, anger, fear, disgust, sadness, empathy, beauty, "union with God" (induced with ayahuasca), happiness, inequity, and more (Craig, 2009).

The role of the insula, however, is not limited to sensory and emotional functions. Studies have also found its involvement in learning and decision making and a number of experiments have identified insular activity that co-varied with value or value-related features of choices. Seymour et al. (2004) showed that subjective value in a temporal decision model selectively correlated with activity in the right anterior insula. Preuschoff et al. (2008) showed that bilateral insular activations coded for both risk and risk prediction errors. In a task in which participants made purchase decisions, Knutson et al. (2007) showed that the insula was activated when prices were in excess of expectations. Apart from higher order economic decisions, several studies also pointed at the insula's role in perceptual decision making, time perception, and cognitive control (Craig, 2009).

Finally, the insula's involvement in representing sensations, feelings, and evaluations about such sensations elicits the hypothesis that the insula might be engendering consciousness itself (Craig, 2009). The van Economo neurons (VEN), unique to the insula and the ACC, are known to selectively and severely atrophy in cases of frontotemporal dementia (Seeley et al., 2006). Subjectively, this is accompanied with a sense of loss of emotional awareness. Nimchinsky et al. (1999) showed that there are progressively fewer VENs from humans to bonobos to gorillas, and they are virtually absent in arthropods. This phylogenetic gradation parallels the mirror test for self-awareness, sometimes described as the Rubicon of self-awareness (De Waal, 2008). Even within humans, Allman et al. (2005) showed that VENs increase with age until children turn four. They also proposed that in autism spectrum disorders, VENs fail to develop normally, leading to impaired social ability and faulty intuition.

The insula is also linked to tracking background reward in studies of decision making. Wittmann et al. (2020) showed that bilateral insular activations tracked global reward states when macaque monkeys made decisions, and the insular pattern of activity was distinct from that observed in the DRN.

Dorsomedial prefrontal cortex

The dorsomedial prefrontal cortex (dmPFC) is located in the most frontal part (the prefrontal cortex) of the human brain. It comprises areas 9 and 10 of the Broadmann taxonomy (Lieberman, 2013), however other researchers also include areas 8, 11, and 32 in their classification (Leary and Tangney, 2012).

Successful social interactions not only require us to act ourselves, but also to monitor the actions of others in an environment. The dmPFC plays a key role in social cognition, especially in observing and tracking others and their social context

(Wittmann et al., 2018). Yoshida et al. (2011) set up a decision making task in which monkeys chose between two options, one that would be rewarded and one that would not. However, in addition to the monkey making the choice, they positioned another monkey in an observer role. Throughout the task, the actor and observer monkeys switched roles, allowing the researchers to delineate neural regions implicated in action versus observation. The authors found that neurons predominantly in the dmPFC (but also the ACC) were involved in observation of others but not of oneself. This finding corroborates well with fMRI studies in humans. For example, Wittmann et al. (2016) found that the area9 dmPFC not only tracks others' performance, but also responds to whether the social context is competitive or collaborative.

The dmPFC not only tracks others' actions, but it also contributes to the production of behavioural strategies that are difficult for others to predict. Seo et al. (2014) trained 3 rhesus monkeys to perform an oculomotor decision making task modelled after the matching pennies task against a computer opponent. The monkey received a token when it made the same choice as the computer, and six tokens led to a juice reward. The computer, however, was programmed to exploit the monkeys' behaviour by adapting to its past choices. Therefore, the optimal strategy for the monkey meant maintaining unpredictability in its choices.

Seo et al. (2014) found that the animals were more likely to stay on their previous choice if they received a token, and more likely to switch if they lost one. Further, they found that neurons in the dmPFC tracked animals' choice and reward history, which was representative of the computer's exploitative strategy. They also found that when animals deviated from heuristic learning algorithms, switching signals in the dmPFC reflected this tendency. This suggests an overarching role of the dmPFC in tracking the environment and determining when to switch from typical reinforcement learning patterns.

All in all, we have now surveyed the key regions of interest that might be involved in representing background statistics of social environments — namely the DRN, hypothalamus, Hb, SN, VTA, insula, and dmPFC. In the next section, we will investigate whether and how social decisions in various environments might be linked to our mental health.

1.4 Mental health and social affiliation

Classification

We now turn our attention to the influence of social connections on our mental health. I will describe the way mental health conditions are classified, and then go into detail about the conditions that might most respond to social connection—namely affective disorders like depression and anxiety. Next, I will conclude with a discussion on social media and mental health.

There are two major classification systems that dominate research in psychiatry: the diagnostic and statistical manual of mental disorders (DSM) and the International Classification of Disease (ICD) (Murray et al., 2008). Both of these systems provide detailed descriptions of all major types of psychiatric disorders like personality disorders, affective disorders, and other behavioural dysfunctions. They do, however, differ in how they are structured. The DSM-V, the latest version of the DSM, consists of operational definitions of various disorders, and the emphasis is on specifying clear diagnostic criteria for practicing clinical professionals. The ICD-11, on the other hand, largely emphasises theoretical descriptions of mental disorders but does come with a separate manual to help with implementation in clinical practice. The ICD is a system of classification of all illnesses, not just mental health disorders, whereas the DSM is specifically designed for classifying psychiatric disorders.

In clinical settings, the process of diagnosis is largely interview based. When a person presents with a complaint, a psychiatrist conducts an interview, tries to form picture of their mental experience, and then ascribes a diagnostic label as they deem appropriate (Murray et al., 2008). Clinicians also often use self-report questionnaires to aid their assessment of the nature and severity of presenting symptoms. Such questionnaires include the Beck's Depression Inventory for assessing symptoms of general depression (Beck et al., 1960) and Autism Spectrum Quotient test for assessing symptoms of autism (Baron-Cohen et al., 2001). While such questionnaires can help, they only capture subjective experience, and the clinician has to use their judgement to make an objective assessment about the intensity and nature of individual symptoms.

Because mental disorders are defined by grouping various affective, cognitive, and behavioural symptoms, the various diagnoses are in fact “syndromes” and not “diseases” (Murray et al., 2008). For something to be classified as a disease, it requires a demonstration of observable pathology, which is not possible in most psychiatric conditions, at least not yet. While the DSM and ICD are internationally accepted, it must be noted that they are still a “best guess”, and they need to be continually updated and modified with our growing knowledge of mental disorders.

While diagnosis with DSM and ICD have proven to be reliable over the years, a symptoms-based classification approach to mental disorders has its downsides. First, it can suffer from the problem of heterogeneity, because people can qualify for a single diagnosis in multiple ways (National Institute of Mental Health, 2021). For instance, two people can be diagnosed with the same disorder, but may still have few symptoms in common. Next is the problem of comorbidity, in which people who meet the criterion for one disorder could also meet the criterion for another. Finally, the clinical criteria for what counts as a pathological level of symptom occurrence, while agreed through expert consensus, is still chosen arbitrarily.

To overcome these problems, a third way of classifying mental health disorders is proposed: Research Domain Criteria (RDoC) (Cuthbert and Insel, 2013). The RDoC does not approach mental disorders as symptom-based complexes derived from clinical descriptions. Instead, they invert the process; basic sciences—areas like genetics, neuroscience, and psychology—are taken as the starting points and the disorders are considered as disruptions of normal psychophysiological process. As the authors put it: ‘ the RDoC is committed to studying the full range of variation, from normal to abnormal.’

The RDoC have adopted 6 categories, or “domains”, to classify psychophysiological systems: negative valence, positive valence, cognitive systems, systems for social processes, arousal/regulatory systems, and sensorimotor systems (Cuthbert and Insel, 2013). Within each system, there are individual constructs that make up that domain. For example, the domain of ‘negative valence’ comprises systems responsible for aversive situations, like anxiety and fear. This structure of domains, and individual constructs within domains, creates a matrix of behavioural and biological systems, which can be used to classify mental disorders.

Finally, the recent past has seen an emergence of data-driven methods that draw diagnostic boundaries based on algorithmic classification from large datasets (Gillan and Seow, 2020). This approach uses normal variations of psychopathology in the general population to define new dimensions of mental illnesses using data-driven methods. Such an approach, therefore, also represents a shift away from using clinical interviews as the quintessential diagnostic method, and toward using self-reported assessments, which are more scalable and minimise problems associated with inter-rater reliability.

Gillan et al. (2016) developed one such data-driven classification method out of necessity to resolve issues of specificity that arose in their experiment on OCD. In their study, they faced a problem: while deficits in goal-directed behaviour were a characteristic symptom of OCD, several studies also showed similar deficits in other disorders (Gillan and Seow, 2020). This suggested that goal directed deficit either may not be specific to OCD and therefore may have limited explanatory potential, or the classification itself represented a flawed separation of categories. In other words, there was a possibility that goal-directed behaviour might be best captured as a separate dimension of mental health.

Gillan et al. (2016) recruited over 1400 individuals to complete several mental health measures of eating disorders, social anxiety, impulsivity, alcohol addition, and indeed OCD (and more). A factor analysis revealed a simpler three-factor solution that accounted for intercorrelation between multiple clinical dimensions. These factors were the following: social withdrawal, anxious depression, and compulsive behaviour and intrusive thought. Further, the compulsive dimension was associated with deficits in goal-directed control measured through a separate behavioural task. This result provided external validity to the newly defined construct, and subsequent studies have attested to the robustness of the factor-analysis driven classification (Gillan and Seow, 2020).

In one of my experiments[4], I will use this approach to create trans-diagnostic factors and investigate whether they better explain social decisions. But first, in the sections to follow, I will describe symptoms, neurobiology, and treatments associated with traditionally classified illnesses relevant to social decision making such as depression, generalised and social anxiety, and more. I will then end this chapter with a discussion on a new class of decisions, the ones we make online on social media, and its potential impact on mental health.

Depression and affective disorders

Depressive symptoms are some of the most common symptoms that present in medical care. In fact, the prevalence of depressive symptoms is only second to those involving physical pain (Murray et al., 2008). Bebbington et al. (1989) estimated the risk of depression and suggested that 7 out of 10 women and 4 out of 10 men will experience minor episodes of depression at least once in their lifetime. Like most other psychiatric disorders, depression is classified and diagnosed based on patients' signs and symptoms, and there is no objective pathophysiology or reliable diagnostic test currently present.

In a large study with over 1000 participants, Korszun et al. (2004) identified the frequency of symptoms that accompanied episodes of depression. Amongst such symptoms, the loss of the ability to experience pleasure, also known as anhedonia, was present in almost all patients in the study. In such cases, people experience

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[4] relationships-between-mental-health-and-personality-profiles-and-the-influence-of-environmental-factors-on-social-engagement

diminished joy from activities they or others normally enjoyed, and there was an absence of pleasure from work, play, or food. When in depressive episodes, such people also experience a diminished libido and disturbed sleep, which included the inability to fall asleep (onset insomnia) and disruptive awakenings (maintenance insomnia).

Another common symptom in depressive disorders is a lack of vigor, drive, or energy (Korszun et al., 2004). Such symptoms are often referred to as apathy. Patients experiencing apathy report a lack of interest, and difficulty sustaining attention. On a day-to-day level, such patients complained about difficulties reading a newspaper article or understanding a movie plot (Murray et al., 2008). Slowness of movement may also be observed, which is also referred to as psychomotor retardation.

Fried and Nesse (2015) analysed symptoms reported by 3703 depressed outpatients from the "Sequenced Treatment Alternatives to Relieve Depression" (STAR*D) study and found as many as 1030 unique symptom profiles. The top symptom profile, comprising all diagnostic symptoms of depressions except suicidality and hypersomnia, was observed in only 1.8% of the individuals. In other words, there is substantial variation in symptoms in patients that all qualify for the same diagnosis (in this case, depression).

Both the ICD and DSM provide diagnostic criterion for depression, but they differ in some minor ways (Murray et al., 2008). The DSM contains a single category of major depression, whereas the ICD breaks down depressive episodes into mild, moderate, and severe types. While there are small differences in wordings between these two systems, the overall array of symptoms is largely similar. The one symptom that the ICD includes but DSM does not is loss of confidence or self-esteem. The DSM, however, needs the symptoms to cause "clinically significant distress or impairment" but the ICD does not. Both explicitly exclude manic episodes from their diagnostic criteria.

While the DSM and ICD might appear to provide an objective assessment for depression at first, studies show that there is minimal agreement between clinicians on their diagnoses (Lieblich et al., 2015). In an attempt to create more objective assessments, several inventories and questionnaires have been proposed. The Beck's Depression Inventory (BDI) is one of the most common inventories used in clinical and research contexts (Beck et al., 1960). Studies have further broken down the BDI in somatic, cognitive, and affective subscales (Vanheule et al., 2008). Other instruments used to assess depression include the Hamilton Depression Rating Scale, Patient Health Questionnaire, and more (APA, 2024).

The neurochemistry and treatment of depression remains an active field of investigation. It was first found that reserpine, a drug that depleted monoamines in the brain, induced depression in healthy patients, and as a result depression was thought to be a result of monamine depletion (Coppen, 1967). This hypothesis was quickly challenged when the precursor to serotonin L-trypotophan was shown to have antidepressant effects. Indeed today, selective serotonin reuptake inhibitors (SSRI) are the most common first-line treatment for depression (Murray, 2007).

The idea that depression is a result of abnormalities in the brain is prevalent amongst clinicians and the public alike. Pilkington et al. (2013) showed that up to 80% of the Australian population believed that depression is caused by chemical imbalance in the brain. Moncrieff et al. (2022) undertook a systematic review of studies supporting the "serotonin hypothesis" of depression, and found that meta-analyses (largest n=1845) showed little to no relationship between serotonin depletion and depression. Some studies even showed a lowered serotonin concentration following anti-depressant use. The authors therefore concluded that there was "no consistent evidence of there being an association between serotonin and depression." Smith et al. (2024) have argued, however, that there are concerns about the inclusion and exclusion criteria of studies included in the aforementioned meta-analysis.

Nevertheless, it seems likely that a disease as complex as depression will not be explainable simply by a single factor such as reduced serotonin levels (Cowen and Browning, 2015). Fountoulakis and Tsapakis (2024) noted that despite the absence of a simple link between serotonin depletion and depression, the fact that SSRIs work to reduce symptoms of depression remains indisputable. Arnone et al. (2024) suggested that while serotonin depletion alone does not explain the complexities of depression, it does not mean that serotonin is not involved in depression at all. Direct measurement of serotonin requires advanced and recently developed neuroimaging methods such as Positron Emission Tomography (PET), and the current absence of a link between serotonin and depression might be 'nescience in disguise'. Indeed, when using a novel serotonin receptor antagonist in Positron Emission Tomography (PET), Erritzoe et al. (2023) found the first direct evidence of reduced serotonin levels in patients experiencing major depression. With the methods of cognitive neuroscience like optogenetics, PET, and fMRI constantly improving, only future studies might be able to disambiguate the role of serotonin in depression.

For all the discussion about neurochemistry, it is worth noting that the first line of treatment for mild to moderate depression is often psychotherapy. Butler et al. (2006) reviewed over 300 published studies and 15 meta-analyses on cognitive behavioural therapy (CBT) and found large effect sizes for CBT compared to placebo in patients receiving treatment for major depression. Compared to antidepressants, CBT seemed to be as effective if not slightly better in treating cases of adult unipolar depression. Elkin (1989) suggested that CBT may be inferior to anti-depressants for treating severe cases of depression. Besides CBT, other styles of therapy like interpersonal psychotherapy, internal family systems therapy, and mindfulness-based cognitive therapy have showed varying degrees of efficacy (Haddock et al., 2017). In cases of moderate to severe depression, a combination of medication and psychotherapy might be most likely to have the best treatment outcome (Cuijpers et al., 2020).

Neuroimaging studies have revealed some unique markers of depression. There is evidence of reduced hippocampal volume in patients suffering recurring episodes of depression but not in those who have suffered only one (Campbell and MacQueen, 2004). Fu et al. (2004) showed that patients with major depression had increased amygdalar activation in response to sad faces. Godlewska et al. (2016) reported greater activation in the anterior insula and dorsal anterior cingulate cortex (ACC) in response to fearful versus happy faces in depressed patients. Further, 7 days of escitalopram (an SSRI) led to a reduction in activation in regions like the insula, ACC, amygdala and thalamus in patients who responded to anti-depressants. In addition to localised changes in brain regions, depression has also been associated with unstable and altered functional connectivity in brain networks like the default mode network (Wise et al., 2017).

Motivation, learning, and reward processing are some of the key behavioural processes affected in depression. Naturally, both serotonergic and dopaminergic systems are postulated to modulate such adaptations (Lan and Browning, 2022). This has led to a rise in using reinforcement learning models to explain depression using computational methods. Huys et al. (2015) have proposed a decision theoretic account of depression, whereby depression could be assessed through impaired decision making, and that such deviations could be explained through computational methods. These methods could yield mechanistic pathways that lead to depression, for instance a reduction in vigour, biased utility estimates, or inaccurate state inferences.

Recent research investigating the behavioural processes affected by depression has progressed from using simple experimental tasks to those that incorporate more ecological features (Scholl and Klein-Flügge, 2018). For instance, one search feature is how humans differentially learn in stable and volatile environments. Behrens et al. (2007) found that humans modulated their learning rate based on their decision-making environment; they learned faster in volatile environments and slower in stable environments. Further, Blain and Rutledge (2020) found that subjective happiness was related to learning-related variables, and depressive symptoms were related to reduced happiness in volatile environments.

Overall, depression is a complex illness and its aetiology and treatment remains a field of constant inquiry.

Generalised and Social Anxiety, and Loneliness

Anxiety disorders are the most prevalent mental health conditions in both the developed and the developing world (Murray et al., 2008). The word anxiety is derived from the latin word anxietas, which means worry or carefulness. Modern use of the word is thought to encompass the affective, behavioural, and cognitive responses to the perception of danger (Murray et al., 2008). In addition to the suffering caused to the patients, these disorders also carry a significant economic burden (Greenberg et al., 1999).

While anxiety disorders are psychiatric disorders, anxiety in itself is considered a normal phenomenon and even required for day-to-day living (Murray et al., 2008). When a person's level of anxiety exceeds a threshold such that the arousal becomes maladaptive, that's when they are said to have an anxiety disorder. These disorders are categorised into generalised anxiety disorder (GAD), social anxiety disorder (SAD), panic disorder (PD), and posttraumatic stress disorder (PTSD). While the diagnostic criteria differ, anxiety disorders tend to co-occur with each other or with major depression.

The diagnoses for GAD require a core symptom of uncontrollable worry to be present for a majority of days in a six-month time span (Murray et al., 2008). In addition, these psychological symptoms need to be accompanied with physical symptoms like chills, palpitations, and nausea. The six-month timeframe has been challenged for its arbitrariness, and Kessler et al. (2005) have argued that there is no substantial difference in symptoms for patients that have suffered for fewer than six months.

On the other hand, PDs are characterised by unexpected and episodic panic attacks (Murray et al., 2008). Symptoms of panic attacks include a pounding heart, trembling or shaking, feeling of choking, chills, and fear of losing control, amongst others. Fear of subsequent panic attacks also is a feature of PD. A large majority of patients suffering from PD also suffer from agoraphobia, characterised by a fearful anticipation of situations where one will find withdrawal or escape difficult (Goodwin et al., 2005).

Social anxiety disorder (SAD, also known as social phobia) is marked by a stifling fear of social interaction or social performance (Murray et al., 2008). People experiencing social anxiety disorder often fear embarrassment or rejection. Its prevalence is reported to be between 3–16% in population-based studies. Typically, such social fears are triggered in social situations like talking in small groups, dating, etc., and also in performance situations like public speaking. In some cases, these socially-triggered fears may escalate into a full-blown panic attack. Since the onset of SAD is around teenage or early twenties, the impact on psychosocial development is substantial. For example, people with SAD are more likely to have fewer friends and remain unmarried (Murray et al., 2008).

Posttraumatic stress disorder (PTSD) is a unique anxiety disorder because it needs a triggering event to have happened before the onset of symptoms (Murray et al., 2008). Community studies have shown a lifetime prevalence of about 1% (Davidson et al., 1991). Symptoms of PTSD include recurring and intrusive recollection of the traumatic event, intrusive dreams about the event, and avoidance of images, thoughts, or feelings regarding the event. It is worth noting that only a small percentage of cases (less than 12%) who experience a traumatic event will end up developing PTSD.

Like most psychiatric conditions, anxiety disorders are thought to have a biopsychosocial pathogenesis (Murray et al., 2008). Mochcovitch et al. (2014) reviewed neuroimaging findings and found that emotion dysregulation in GAD patients was associated with prefrontal cortex and ACC hypofunction, and decreased cortex-amygdala functional connectivity. Neurochemistry studies have hinted at the roles of serotonin-based systems. For instance, Garvey et al. (1995) found that severity of anxiety symptoms predicted levels of a serotonin metabolite. Selective serotonin re-uptake inhibitors are considered first line of treatments, also hinting at a potential role of serotonin in anxiety disorders (Murray et al., 2008).

Another neurotransmitter implicated in anxiety disorders is noradrenaline (NA;

also known as norepinephrine) (Murray et al., 2008). NA is primarily synthesised in the locus coeruleus (LC), a tiny structure in the brain stem, and is projected from the LC to the prefrontal cortex (PFC). NA is known to modulate cortical function during periods of stress, arousal, attention, vigilance, and more (Bouras et al., 2023). Under normal circumstances, NE release keeps neurons in an "awakened" state, however hypo-arousal of the system can lead to drowsiness, and hyper-arousal can lead to vigilance or anxiety like behaviours.

The PFC is thought to regulate behaviours through its rich connections to circuits involved in non-pathological anxiety and fear conditioning like the amygdala (especially the basolateral amygdala and the central amygdala), bed nucleus of the stria terminalis (BNST), striatum, and insula (Calhoon and Tye, 2015). In clinical cases of anxiety, amygdala hyper-activation is consistently observed (Etkin and Wager, 2007). Bouras et al. (2023) proposed that hyperfunction of the NA system led to hyper-arousal and a loss of top down PFC control on regions implicated in fear, which in turn led to a pathological state of anxiety.

Within the amygdala, the neurotransmitter gamma-aminobutyric acid (GABA) is thought to modulate anxiety-related responses (Gauthier and Nuss, 2015). For example, Sanders and Shekhar (1995) injected GABA receptor antagonists in the basolateral amygdala (BLA) of rats and found that it led to anxiety-like effects. Similarly, they infused a GABA agonist in the central amygdala (CeA) and found that it led to anxiolytic effects. In humans, the benzodiazepine Lorazepam led to a deactivation in the amygdala when people completed an emotion processing task (Paulus et al., 2005).

Similar to major depression, the treatment of anxiety disorders involves a combination of psychotherapy and pharmacotherapy (Murray et al., 2008). CBT remains the main modality of therapy to help with anxiety disorders. Benzodiazepines and SSRIs are common psychotropic agents prescribed for anxiety disorders.

All in all, the aetiology and treatment of anxiety disorders remains an active field of study.

Social media and mental health

In chapter two, I will present a laboratory-based task in which people send friend requests to others in different environments. Such laboratory-based tasks are normally criticised for lacking ecological validity, especially in social domains where having real world interactions make controlling for variables difficult and neuroimaging impossible. However, the rise of social media has paved the way for a new kind of social interaction, and might also confer a unique kind of ecological validity to a laboratory-based social affiliation task. Given the resemblance between social media and a friend request sending task, I will review some recent literature on social media and its impact on mental health.

Social media is a novel and unique way of social interaction that has emerged in the past decade or two. While social media has become a day-to-day part of many people's lives, the research on the safety of its use remains scant. Haidt (2024) has argued that the effects of social media are particularly damaging for young adults, or Gen Z, defined as the generation born after 1995.

Haidt et al. (2024) have reviewed a number of population-based studies that link social media usage to adverse mental health measures. For instance, Twenge et al. (2018) analysed representative surveys of U.S. adolescents (N=506,820) and found that those who spent more time on social media were more likely to report mental health issues. Similarly, Twenge and Campbell (2019) analysed surveys across multiple countries, and found that light users of digital media (including, but not limited to, social media) reported higher well-being and happiness. Those who spent most time on social media also tended to exhibit a higher occurence of mental health markers like suicide risk, and were twice as likely to have reported an attempted suicide. In the UK, Kelly et al. (2018) reviewed data from the UK Millenium Cohort Study (N=10,904 14 year olds) and found social media use was associated with higher depressive symptoms, and that this effect was especially strong for girls. Primack et al. (2017) found higher social media use was associated with increased loneliness. It is worth noting that Orben and Przybylski (2019) have criticised the above associations citing that they are derived from analysis of secondary sources, and depend heavily on how researchers defined terms such as "depression" or "technology usage".

Population studies, however, can only establish a correlation, and skeptics also point at the lack of causal evidence linking social media use to mental health outcomes. In the recent past, several experimental studies have started to provide evidence of causation. Hunt et al. (2018) made undergraduate participants from the University of Pennsylvania limit their social media use to 10 minutes per day for 3 weeks. They found that the limited use group showed decreased loneliness and depression markers compared to a control group and decreased anxiety and fear of missing out over their own baseline. Similarly, Allcott et al. (2020) had over 2,700 adults deactivate their Facebook account for four weeks, and found that this intervention led to increased subjective well-being, time spent with family and friends, and reduced online activity even on other social media sites. Brailovskaia et al. (2023) also found that reducing social media use by 30 minutes led to fewer depressive symptoms, reduced COVID-19 burden, and increased life satisfaction.

Kleemans et al. (2018) asked 144 girls (14 to 18-year-olds) to look at Instagram selfies that were either original or manipulated (retouched and reshaped). They found that looking at the manipulated images led to a reduced body image and that this effect was especially stronger in girls who showed a higher sensitivity to social comparison prior to the experiment. Similarly, Engeln et al. (2020) asked 308 undergraduate women to use Facebook, Instagram, or a matched control game. They found that spending as little as seven minutes on Instagram, but not Facebook, led to a decrease in body image. Such studies highlight that not all social media might be affecting children and young adults in the same way, and more work needs to be done to dissociate the effects of different platforms on different groups.

Despite the ill-effects of social media, it continues to attract billions of daily users. Such popularity is often thought to be caused by a need to belong and gain social rewards, and leads to the hypothesis that social media behaviour could be characterised as a modern day Skinner Box. Lindström et al. (2021) analysed over one million posts from over 4000 individuals made on social media using computational methods drawn from reinforcement learning theory. They found that social media usage conforms well to the principles of reinforcement learning, and that specifically users timed their posts such that it minimised effort costs and maximised social rewards. Further, in an online experiment (n=176), the researchers showed that social rewards causally influence behaviour, in accordance with predictions from their model.

While early studies are providing compelling evidence for the role of social media in promoting mental ill-health, not all studies have seen this causal link hold true. For example, Hall et al. (2019) made participants abstain from social media use for a number of weeks and found no evidence of altered mental health. Haidt et al. (2024) noted that this study might be underpowered as it only tests 26 participants per experimental group. Collis and Eggers (2022) asked participants to restrict their social media use to 10 minutes per day and found no impact on well-being or academic success. A handful of other studies have also reported no to mixed effects (Haidt et al., 2024).

All in all, these early studies are showing that digital interactions through social media hold the potential to reduce our well-being, and especially that of young adults. The exact pathways and mechanisms remain to be determined, and future studies will need to shed light on how social media affects mental health.

1.5 Conclusion

In this chapter, I provided a theoretical overview of the psychology and neuroscience of social decision making. I started by looking into classical studies from social psychology that explored how we form social affiliations. I then looked into classical studies in social neurosciences and described theories like the social brain hypothesis. Next, I described the theoretical accounts from preclinical foraging studies that laid the foundation for behavioural and neural hypotheses for tracking social environments.

Finally, I described the literature on mental health and how it might relate to social decisions. We are now ready to turn to the experimental chapters of this thesis.

Chapter 2

A behavioural assay of social affiliation decisions

2.1 Introduction

Over the past two decades, we have seen extensive interest in human social behaviour and its relationship to our well-being. Studies have overwhelmingly noted a positive contribution of social connection on our well-being. This research, as Dunbar (2018) puts it, has shown that friendship is the "single most important factor influencing our health, well-being, and happiness". While features of individuals like attractiveness and similarity to oneself are known to facilitate interpersonal connection, relatively little is known about whether features of the environment do the same.

Some studies in social psychology hint at the role of the environment in friendship formation with findings such as physical proximity leading to more friendships (Hewstone and Stroebe, 2021). Similarly studies in the foraging literature raise the possibility that affiliation behaviour might vary with the richness of social environments; in these studies, animal foraging behaviour changed as a function of the richness of opportunities for finding food that animals encountered in different patches (Pyke et al., 1977). So perhaps, by analogy, how much one is disposed to "forage for friends" might vary with the richness of social environments. However, whether and how much varying background statistics of social environments would affect social decisions remains unknown.

In the present study, I investigate human decisions to initiate affiliation with other individuals in different environments. I suggest that, despite their importance, the outcomes alone may not sufficiently explain the choices people make. Instead, I suggest that the environment in which we make social decisions might affect the decisions themselves. In particular, I hypothesise that two features of an environment would influence people's decisions to initiate friendships: the friendliness, that is the average success of one's attempts to create friendships in a given environment, and the density, that is the number of opportunities one gets to create friendships in a given environment.

While studies on social affiliation behaviour in different environments are scant, hypotheses on such behaviour can be drawn using analogies from foraging theories. We have seen earlier that animals choose to allocate more resources in energy rich environments (Pyke et al., 1977). We have also seen that animals tend to be more selective in denser patches (Krebs et al., 1977). Taken together, results from foraging theory would predict that people would attempt to initiate more friendships in friendlier environments as compared to hostile environments (i.e. they expend more resources pursuing opportunities when there are more opportunities, for example, in environments that are richer on average), and initiate fewer friendships in denser environments as compared to sparser environments (i.e. they become more selective in denser patches). If people were disinclined to initiate friendships in dense or hostile environments, then their reaction times might still be slower even on occasions when they do initiate a friendship attempt. By contrast, reaction times when participants avoid initiating friendships might be longer in sparse and friendly environments.

An alternative account, primarily motivated by the study of tonic dopamine in decision making, leads to divergent predictions compared to those coming from foraging theory. Niv et al. (2007) suggested that opportunity cost played a major role in influencing a rat's behaviour. When the average rate of reward was high, there was a higher opportunity cost to not acting and therefore they expected a rat to exert more effort to obtain more reward. When the average rate of reward was low, there was a lower opportunity cost associated with not acting and therefore they expected a rat to exert less effort.

It is possible that people would act similarly to minimise the opportunity costs of their actions even when making social decisions. Niv et al. (2007)'s results might predict that people would be more likely to initiate friendships when they are in a dense environment as compared to a sparse environment. Similarly, they would initiate friendships more often in a friendlier environment as opposed to a hostile environment. I would also expect people to be faster in denser and friendlier environments than in their sparser and more hostile counterparts.

In summary, both accounts of animal behaviours, namely Krebbs and colleagues' (1977) study on birds and Niv and colleagues' (2007) study on rats lead to slightly different predictions for social decision making. On the one hand, the optimal foraging model predicts that people would initiate friendships more in friendly and sparse environments whereas on the other hand the tonic dopamine model predicts people would initiate more friendships in friendly and dense environments. In other words, both these accounts make the same prediction for friendliness but differ in their predictions of density.

2.2 Methods

Participants

Ethical approval for this study was obtained through the Medical Sciences Interdivisional Research Ethics Committee (MS-IDREC; ref: R73912/RE001). Informed consent was obtained from each participant before they began the experiment.

Multiple datasets were collected as part of this study, split into a discovery and confirmatory dataset. Participants were recruited using the Prolific recruitment platform (prolific.co).

The initial discovery sample included 300 healthy participants out of which 218 participants (mean age = 25.3, males =110, females = 107, other = 1) met the inclusion criteria. For the confirmatory dataset, an a priori power analysis was conducted using G*Power version 3.1 (Faul et al., 2007) for sample size estimation, based on data from our discovery sample. The smallest effect size of an effect of interest in the discovery study was 0.017. With a significance criterion of = .05 and power = .95, the minimum sample size needed would be N = 767 for a t-test computed using the Pearsons correlation coefficient. Thus, the power analysis suggested collecting a minimum sample of size 997 after accounting for a 30% attrition rate. Thus, for the confirmatory dataset, I collected data from 1018 participants out of which 783 met my inclusion criteria (mean age = 27.3, males = 392, females = 380, other = 11).

Only participants who met the following inclusion criterion were invited to take part in the study:

1. Age was between 18 and 40 years old
2. They had normal or corrected to normal vision

After collecting pseudonymised data through Prolific, the data was checked for completion. Participants who completed the task were paid at the rate of £6/hr for their participation and an additional £2 bonus for task completion.

With all the completed datasets, I further used the following exclusion criteria. These criteria were developed using data from the discovery sample.

Exclusion criteria:

1. Total timeouts (trials in which participants failed to respond after 3 seconds) exceeded 15 in number
2. Request rate per block was either 1 or 0, and that happened for 2 or more blocks out of the total 12.

3. Participants failed to answer repeat questions (a selection of 5 random questions from 5 different questionnaires) presented at the end of the experiment within a 2-point absolute deviation, and this failure of repetition happened for two or more items.

4. Maximum standard deviation of request rates within the same block type was greater than 0.3, which would suggest an inconsistent or random choice strategy within a block type.

5. Task effects were outside 3 standard deviations of their sample means.

The following is the list of participants that were excluded based on the above criteria:

Exclusion Criteria	Number excluded
Total timeouts > 15	28
Multiple blocks with only requests or skips	112
Inconsistent answers to repeat questions	43
Inconsistent request rates	56
Outliers based on task-specific effects	61

Task

A computer based task was coded using jsPsych (de Leeuw, 2015) and was uploaded to the Department of Experimental Psychology's server through "Just Another Tool for Online Studies" (JATOS) (Lange et al., 2015) and Pavlovia (pavlovia.org).

In the instructions prior to starting the task, participants were given a cover story in which they were asked to imagine moving to a new city and make new friends. To help them create connections, they would be taken through different clubs which differ in two respects: the friendliness of the people in the club and the number of people that appear in the club.

Four combinations of clubs were possible: friendly-dense (FD), friendly-sparse (FS), hostile-dense (HD), and hostile-sparse (HS) (see Figure 2.1b). In a friendly club, 80% of all friend requests that a participant sent were accepted whereas in

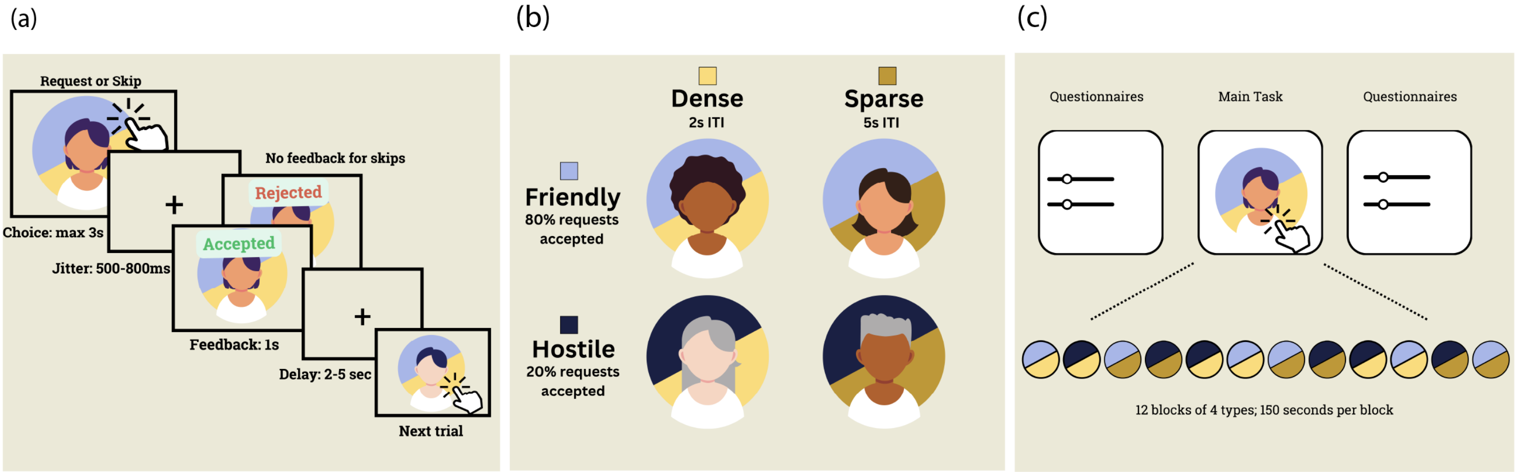


Figure 2.1: Task structure and behavioural effects. (a) schematic representation of a given trial with timings. (b) Our two experimental manipulations: friendliness and density. In a friendly block 80% of friend request sent are accepted, while in a hostile block 20% of requests are accepted. In a dense block, the inter-trial interval is a shorter 2s compared to the 5s interval in a sparse block. (c) Overview of the experimental structure in any given run.

a hostile club, only 20% of all requests were accepted. In a dense club, the time between two consecutive encounters with other club members (being shown a club member face) was briefer; the faces appeared every 2 seconds with a jitter between 400 and 700 milliseconds. In a sparse club, the time between two consecutive faces was 5 seconds with an equivalent jitter.

The background colour of the club (blue or green) indicated the level of friendliness of the club and the background pattern (smaller or larger circles) indicated the level of density of the club. For instance, a blue background with small circles might have indicated a friendly-dense block for some participants. The mapping of backgrounds and patterns to club-type was counterbalanced across participants. At the start of each club, participants were informed about the type of club they would be entering.

Inside each club, participants were shown a series of faces and given the opportunity to send friend requests. The faces presented as stimuli were obtained from the Chicago Faces Database (Ma et al., 2015). The order of the faces was randomised between participants. Participants saw each face only once.

For every face shown on the screen, participants could either choose to send a friend request by pressing ‘j’ on their keyboard or they could choose to skip by pressing ‘k’. Each face would stay on the screen for as long as the participants took to respond, or for a maximum time of 3 seconds. If participants sent a friend request, the next screen would show them whether their request was accepted or rejected. This feedback appeared as text over the face and was shown for a duration of 1 second (see Figure 2.1a for an illustration of trial structure). If they chose to skip, then a fixation cross of the same duration would appear on the screen. If they failed to respond within the stipulated window, a warning sign appeared on screen indicating they were too slow to respond.

Each block (or club) lasted for a duration of 2.5 minutes. Participants were shown a circular timer on the top right of the screen which indicated the elapsed time. The entire experiment comprised a total of 12 blocks, with all 4 types of blocks appearing thrice. The order in which participants encountered these blocks was randomised.

Before the main task began, participants were given a chance to play through 1 practice block to help them familiarise themselves with the design and controls. After they completed the practice block, their understanding of the task was tested with a short quiz comprising 5 questions. They were given 2 attempts to get all questions correct.

At the end of each block, participants were asked three questions. The first question was “How much did you like this club?” and participants indicated their response on a sliding scale from “Not at all” to “Very Much”. The next question was “Did you find a good balance for sending friend requests in this club?” and their responses were taken on a sliding scale from “No, not at all” to “Absolutely yes”. The third and final question was “How do you feel after visiting this club?” and participants indicated their responses on a sliding scale from “Very unhappy” to “very happy”. The purpose of these questions was to get a subjective assessment of how participants viewed the different environments and how they felt while in that club.

After the first pilot (n=19), I noticed that people may not be paying attention to the immediate friendliness of the environment. To make the friendliness salient, I added an attention check in the second pilot (n=10). I asked participants “Did the previous person accept or reject your request” after every 20 seconds. Participants indicated their responses by pressing ‘f’ if accepted, ‘g’ if rejected, and ‘h’ if they skipped the request. This modified version of pilot 2 was then used as the task in the discovery dataset.

Combining this theoretical background with observations of a discovery dataset, I pre-registered the following specific hypothesis (osf.io/62hw7):

(a) People would send friend requests at a higher rate (where request rate is defined as the percentage of trials, out of all trials, on which a request was sent) and will be slower to respond in friendly compared to hostile environments.

(b) People would send friend request at a higher rate and will be slower to respond in sparse compared to dense environments.

(c) People would send friend requests at a higher rate after acceptance than they will after rejections.

(d) People would send friend requests at a higher rate following a previous request particularly in dense environments but may be more likely to make requests following a skip (a non-request) in sparse environments.

(e) People would be faster to skip than to request overall. However, this difference between reaction times will be higher in hostile environments than in friendly environments. Similarly, the difference will be higher in dense environments as compared to sparse ones.

Analysis

Results were analysed and figures were plotted using R v4.3.3 (R Core Team, 2024) running on RStudio v2023.12 (RStudio Team, 2020). Figures were assembled and prepared for publication using Adobe Illustrator v28.4.1 (Ado, 2024).

All binary categorical variables were coded as -1 and 1. Reaction times were log transformed.

A 2x2 repeated measured analysis of variance (ANOVA) was used to examine the effect of friendliness and density on request rates and reaction times. A 2x2x2 repeated ANOVA was used to examine the effects of friendliness and density when the reaction times were further split by action (requests or skips). A similar ANOVA was used to examine the effects of past trial feedback, friendliness, and density on request rates. The normality assumption was examined visually using a quantile-quantile plot. Since all our factors were binary factors, it was not possible to violate the assumption of sphericity.

A linear mixed model was used to also evaluate the same behavioural effects after controlling for gender and attractiveness of the face. Significance threshold for all tests were set at p=0.05.

2.3 Results

Environmental friendliness and density influence social affiliation choices

A 2x2 ANOVA (two levels of friendliness and two levels of density) showed a significant effect of friendliness on request rates (df=782, F=95.7, p=2.17e-21, $\eta_p^2 = 0.109$. See Figure 2.2a). People were more likely to send friend requests when they were in a friendly environment as opposed to a hostile environment. Similarly, density also had a significant effect on request rates. People were more likely to send friend requests when they were in a sparse environment compared to a dense environment (df=782, F=123.5, p=9.77e-27, η_p^2=0.136). Finally, the interaction between friendliness and density was significant (df=782, F=6.7, p=0.01, η_p^2=0.009). People were more likely to send friend requests in sparse environments, but particularly so when in hostile blocks. In a post-hoc analysis, we tested the robustness of these effects by excluding the first 10 trials from every block, and found that the friendliness (df=782, F=59.285, p=4.12e-14, pes = 0.07) and density (df=782, p=8.05e-13, η_p^2=0.063) effects remained

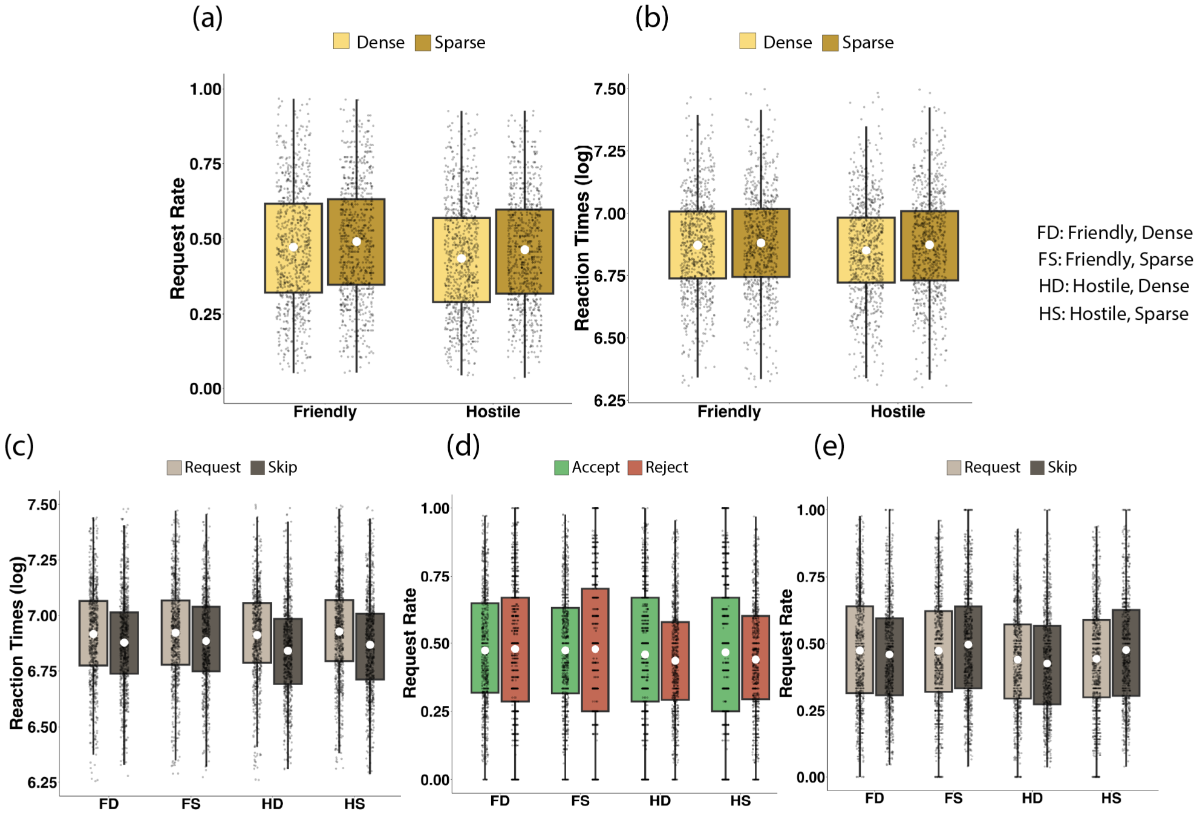


Figure 2.2: Behavioural results. (a) The effects of friendliness and density on request rates. The x-axis indicates the two levels of friendliness, and y-axis indicates the request rate (average number of requests sent) for an individual in that block type. Colour indicates the two levels of density. (b) The effects of friendliness and density on reaction times. Y-axis indicates average log transformed reaction times in the respective block type. (c) Reaction times split into request and skip trials. Colour indicates action (request/skip) (d) The effect of previous trial feedback on choice in the subsequent trial in different environment types. Colour indicates feedback received (accept/reject) (e) The effect of previous trial action on choice in the next trial. Colour indicates action (request/skip).

significant, but not the interaction (df=782, F=2.340, p=1.26e-01 , $\eta_p^2 = 0.003$).

The outcome received on a previous trial ("accept" vs "reject") also affected participant behaviour in the next trial (ANOVA: df=755, F=5.3, p=2.20e-2, η_p^2=7.00e-3; Figure 2.2d). People were more likely to send a request after their previous request was accepted compared to when it was rejected. The interaction between friendliness and previous trial feedback was also significant (df=755, F=7, p=8.00e-3, η_p^2=9.00e-3); people were more likely to send a request following an acceptance, but this was particularly the case in hostile blocks.

Similarly, the interaction between participant choice (request or skip) on the previous trial action and the density was significant (df=782, F=87.4, p=9.21e-20, η_p^2=0.10). People were more likely to send a request following a request in dense environments, but they were more likely to send a request following a skip in sparse environments.

A mixed model ANOVA revealed similar results as above. In addition, both gender (z=2.17–2, p<2e-16) and attractiveness (z=1.46e-2, p<2e-16) also showed significant effects on request rates. These results confirm the replication of all our choice related pre-registered hypotheses.

Environmental friendliness and density influence reaction times in social affiliation choices

Using an analogous 2x2 ANOVA, I found a significant effect of friendliness on reaction times (df=782, F=38.7, p=8.08e-10, η_p^2=0.047; Figure 2.2b). People were slower to respond in friendly compared to hostile environments. Similarly, I found a significant effect of density on reaction times (df=782, F=40.22, p=3.84e-10, η_p^2=0.049). People were slower to respond in sparse compared to dense environments. I also found an interaction between friendliness and density (df=782, F=13.57, p=2.46e-04, η_p^2=0.017). People were slower in sparse compared to dense environments, and this effect was especially pronounced in hostile blocks.

Participants' response type, that is whether they sent a friend request or skipped doing so, also affected their reaction times (ANOVA: df=782, F=103.2, p=7.32e-23, η_p^2=0.12; Figure 2.2c). People were faster to respond if the response was a skip as opposed to a request. There was also an interaction between the response type and friendliness (df=782, F=85.4, p=2.31e-19, η_p^2=0.098). People were faster to skip than to request, but this effect was stronger in hostile blocks compared to friendly blocks. Similarly, there was an interaction between response type and density (df=782, F=20, p=8.92e-06, η_p^2=0.025). People were faster to skip than to request, but this effect was stronger in dense compared to sparse blocks.

These results confirm the replication of all our reaction time-related pre-registered hypotheses.

2.4 Discussion

The aim of this study was to investigate the effect of background statistics of an environment on participants' propensities to initiate friendships. There was a significant effect of both friendliness and density on request rates. Dense blocks had lower request rates compared to sparse blocks and friendly blocks had higher request rates compared to hostile blocks. The background environments also had a significant effect on reaction times. Slower reaction times were associated with sparser and friendlier environments.

The effects on choices conformed well with theoretical predictions from foraging theory. For optimal foraging, birds allocate more resources in abundant environments (Pyke et al., 1977), and this can be considered analogous to people sending more friend requests in friendly environments. Similarly birds show higher selectivity when the encounter rate with the prey is high (Krebs et al., 1977) and this can be considered analogous to people sending fewer requests in denser environments.

While drawing analogies between foraging and social affiliation decisions led to useful predictions of the latter, the parallels with foraging studies are not entirely perfect. For instance, Krebs et al. (1977) originally manipulated the value of each choice by offering birds different types of prey (some worms were small while others were large). Our task differs from the foraging theory experiments in that all faces carried the same reward value (either a request was accepted or rejected). In the future, I could attribute differential values to the faces to see how the relative frequencies of different values impacted choices.

Similarly, Krebs et al. (1977) wrapped the prey in plastic which the birds had to unwrap before consumption. This served as a clear index for the effort birds had to take to get their reward. In our study, participants had only to exert a minimal amount of effort to send a friend request, and consequently there was no clear cost to sending a friend request. While the absence of an effort manipulation makes our task more naturalistic, in the sense that it resembles everyday friend requests, in the future, I could add an explicit cost for sending requests to assess its impact on choices.

In contrast to foraging studies in natural environments, another set of predictions came from laboratory-based studies of operant conditioning. I described the Niv et al. (2007) model, which like foraging theory, proposed that animals made decisions based on the opportunity costs of their choices. However, these two models differed from each other in two important ways. First, the reward the rats received in the Niv et al. (2007) study was of a single type, unlike the various types of reward (different types of worms) birds could access in the foraging theory experiments. Second, the Niv et al. (2007) model emphasised effects of the environment on reaction times as opposed to the choices themselves. While foraging theory suggested that the reaction times might go hand in hand with choice rates, Niv et al. (2007)'s model suggested that the environment creates an independent and direct effect on the reaction times.

In the task, I found evidence for this dissociation between choices and reaction times. Given that people were disinclined to send friend requests in denser environments, foraging theory would have predicted they would act slower in the interest of being more selective. However, I found that people were faster to act in denser environments, thus suggesting that background environment might exert an independent effect on choices and reaction times, as predicted by the Niv et al.

(2007) model.

In this experiment, I favoured a naturalistic design and chose against using an explicit cost for sending a friend request. Despite not having a cost to send a friend request, participants chose to skip sending a friend request multiple times. This is in contrast to rational models of decision making, which would predict that people would send a request to every person they encounter, which would in turn maximise their friendships. How does one explain this “irrational” behaviour?

While it is true that there was no explicit quantified cost for sending a friend request, there was a naturalistic cost in the form of getting a rejection. This rejection would feel unpleasant, and therefore represent an emotional cost for sending a request. Thus, people might be optimising using a different currency of cost, like subjective displeasure. Next, we know from Dunbar (2018) that there is a limit to the number of social ties we can have and maintain. This limit would also represent another constraint that the participants might knowingly or unknowingly account for. Further, in foraging literature, birds seem to act sub-optimally when they forage in equivalent patches with fewer rewards even when familiarised with all available patches (Pyke et al., 1977). This “suboptimal” behaviour has been suggested to be an evolutionary adaptation to protect against fluctuating environments. Therefore, balancing between sending friendship requests or to skip doing so can be viewed as exploration to continually gather information about environments.

2.5 Conclusion

In this experiment, I designed a naturalistic task to test whether and how social environments would affect our decisions to initiate friendships. I showed that background statistics of social environments—namely the friendliness and density of a given environment—influenced one’s choices of initiating social affiliation. People were more likely to send friend requests, and were slower to respond, in friendlier and sparser environments. Previous trial outcome (“accept” vs “reject”) and the interaction of density with previous trial choice (“request” vs “skip”) also affected subsequent trial choices. Finally, I discussed the implications of these results in relation to predictions from animal foraging theories and highlighted places where future work can be done.

In the following chapter, I will discuss how these social decisions might relate to our personality and psychiatric profile.

Chapter 3

Relationship between mental health and social affiliation decisions

3.1 Introduction

Social connection is shown to have positive influences on our physical and mental health, and is also proposed to be a fundamental human need (Hewstone and Stroebe, 2021). On the flipside, a lack of perceived social connection, otherwise known as loneliness, leads to impaired executive functioning, sleep, and eventually an increased mortality risk (Cacioppo and Cacioppo, 2014a). Adverse social factors, alongside biological and psychological factors, are thought to contribute to the development of mental illnesses, and several mental illnesses comprise social symptoms like increased withdrawal (Murray et al., 2008). All in all, there seems to be a link between one's personality and psychiatric profile, and their social decision making.

However, little is known about how this link between mental health and social decisions varies from individual to individual, and whether variation in sensitivity to the social environment plays any role in shaping this link. Moreover, it is unclear whether a lack of social thriving is best thought of as a separate category of ill-health, or simply a symptom of traditional diagnostic categories like depression.

Building on the previous study, in this study I will examine the relationship between people's social preferences in changing environments and their mental health and personality profile. To assess state and trait mental health, I will ask people to complete more than 100 items from multiple standardised questionnaires that measure symptoms for conditions ranging from depression to anxiety to loneliness.

A major limitation of traditional mental health diagnostic categories is the arbitrary distinction between health and disease. There is often uncertainty about specific symptoms or biomarkers that validate the existence of traditional psychiatric categories. As a result, traditional diagnoses of mental health conditions have increasingly been challenged, and researchers in psychiatry are moving towards a trans-diagnostic categorisation of mental health conditions (Gillan and Seow, 2020).

One such approach, developed by Gillan et al. (2016), uses factor analysis to define new dimensions of mental health categories from observed, correlated items of traditional mental health categories. As a result, large number of traditional categories can be reduced to a small number of data-driven categories. This approach is more scalable as it uses self-reported measures as opposed to clinical interviews, and also carries the potential of eliminating inter-rater discrepancies.

Gillan et al. (2016) further showed that such factors can be externally validated using behavioural tasks. In their study, one newly derived factor relating to compulsive behaviour was related to deficits in goal directed behaviour in a computerised task. Similarly, Scholl et al. (2022) found that decision inertia, that is, the tendency to persist longer than appropriate, was linked to a factor representing apathy. Wise and Dolan (2020) showed that enhanced safety learning, a measure derived using computational models of aversive learning processes, was linked to a trans-diagnostic factor representing compulsivity. In this experiment, I intend to derive similar social and non-social factors, which I then expect would be linked to aspects of social decision making in changing environments. I expect factors corresponding to social thriving to be linked with social task measures like total friend requests sent, and factors corresponding to depression or pleasure to be linked to measures like the friendliness effect on choices.

More specifically, based on observations from a discovery dataset, we pre-registered the following hypotheses:

Distinct factors from personality and mental health questionnaires should be identifiable, that load onto behaviours related to:

- Social Thriving
- Obsession/Compulsion
- Social Pain
- Sensation seeking/Urgency
- Pleasure
- Depression-Anxiety
- Impulsivity

In addition, individual variation in these factors should be predicted by individual variation in task measures. More specifically:

Total requests should relate to factors of social thriving and social pain in the following directions:

- Positively to social thriving
- Negatively to social pain

Total requests should relate to non-social factors in the following manner:

- Positively to sensation seeking
- Positively to pleasure

In a discovery sample, I found that social thriving and sensation seeking were correlated. I then hypothesised that sensation seeking would mediate the relationship between social thriving and total requests. I found a trend (p=0.08) for this mediation using a Sobel test. With a larger sample size, we expected this relationship to hold true. So, I predicted that:

- Sensation seeking would mediate the effect of social thriving on total requests.
- Next, the density effect on reaction times would relate:
- Positively to social thriving
- Positively to sensation seeking

As for the previous hypothesis, I expected the relationship between the density effect on reaction times and social thriving to be mediated by sensation seeking.

Finally, the friendliness effect on choices to request or skip social engagement was expected to relate:

- Positively to pleasure

3.2 Methods

Participants

Participants were the same as those described in the previous chapter, and they were subjected to the same inclusion and exclusion criteria. In brief, 218 participants (mean age = 25.3, males =110, females = 107, other = 1) were included in the discovery dataset and 783 were included in the confirmatory dataset (mean age = 27.3, males = 392, females = 380, other = 11).

Task

I used the same task as described in the previous chapter, in which participants were presented with a series of faces and made a decision to send a friend request or to skip doing so. In addition to the behavioural task, participants completed a series of standardised questionnaires to assess their psychiatric profile.

Each questionnaire had a lower time limit of 2 seconds per question to ensure participants took adequate time to understand the questions. If participants completed a questionnaire before this lower time limit, they were given a warning that asked them to reconsider their responses.

Based on my hypotheses, I asked participants to complete a set of social and non-social questionnaires. For obtaining social measures, I used the Lubben Social Network Scale (LSNS) to measure objective social network size (Lubben et al., 2006). The LSNS comprises two subscales: friends and family. Next, I included the UCLA loneliness scale version 3 (UCLA) to measure people's subjective sense of loneliness (Russel, 1996). This scale comprises thriving, lack of connection, and basic connection as its three subscales. Next, I included the Social Connectedness Scale (SCS) to measure participants degree of feeling socially connected (Lee and Robbins, 1995). The SCS breaks down into social assurance and connectedness subscales. I also used the Relationship Questionnaire (RQ) to measure participants attachment styles (Bartholomew and Horowitz, 1991). The RQ comprises subscales measuring four attachment styles: secure, preoccupied, fearful avoidant, dismissing avoidant.

In earlier pilots, I included the Liebowitz Social Anxiety scale (LSA) to measure social anxiety (Liebowitz, 1987; Wise and Dolan, 2020), and the Social Network Index (SNI) to measure social network size (Cohen et al., 1997). However, these scales were discontinued in the main study in the interest of making the task quicker, and after verifying that their inclusion or exclusion did not notably alter the results of the factor analysis that is reported next.

Social well-being is also impaired in general mental health conditions like depression and anxiety. To measure such non-social conditions, I included the Apathy Motivation Index (AMI) to measure apathy (Ang et al., 2017). The AMI comprises social, emotional, and behavioural subscales. Next, I included the Beck's Depression Inventory (BDI) (Beck et al., 1996) and the Snaith-Hamilton Pleasure Score (SHAPS) to measure depression and its associated symptom of anhedonia (Snaith et al., 1995). The BDI comprises somatic, cognitive, and affective subscales (Buckley et al., 2001), whereas the SHAPS comprises sensory, personal, and other-related types of pleasure.

I also included the Rosenberg Self-Esteem scale (RSE) to measure self-esteem (Rosenberg, 1965) and the revised Learned Helplessness Scale (LHS) to measure learned helplessness (Quinless and Nelson, 1988). The LHS breaks down into perseverance, confidence, and helplessness subscales.

I controlled for symptoms of obsession and compulsion using the checking and neutralising subscales of the Obsessive Compulsive Inventory revised (OCI) (Foa et al., 2002). I controlled for impulsivity using the Urgency, Premeditation (lack of), Perseverance (lack of), Sensation Seeking, Positive Urgency, Impulsive Behavior Scale – short (UPPSP) (Cyders et al., 2014), and anxiety using the State-Trait Inventory of Cognitive and Somatic Anxiety (STICSA) (Grös et al., 2007). The UPPSP has sensation seeking, positive urgency, negative urgency, lack of premeditation, and lack of perseverance as its subscales. Likewise, the STICSA consists of somatic and cognitive subscales.

In some earlier pilots, I controlled for symptoms of autism using the Short Autism Questionnaire (AQ) (Allison et al., 2012). However, again, this questionnaire was dropped in the confirmatory dataset in the interest of decreasing the study run time.

Questionnaires were presented in two sets. The first set, comprising SHAPS, UCLA, BDI, LHS, AQ, RQ, PSQ, SPQ, were presented before the behavioural task commenced. The second set, comprising SCS, OCI, LSNS, AMI, UPPSP, LSA, STICSA, was presented after the task ended. In addition, 5 pre-selected items from these questionnaires were presented again at the end of the study with the intention of using them for data quality checks.

Analysis

A factor analysis was used on sub scales of all questionnaires (Gillan and Seow, 2020). First a scree test was used to determine how many factors were to be sought, and then the factors themselves were obtained using a promax rotation and a minimum residual factoring method. The scores from these factors were then extracted using the Thurnstone method (DiStefano et al., 2009). A Pearson's correlation was used to assess the strength of the association between these factors and behavioural measures. A Sobel test was used to carry out mediation analysis.

Some questionnaires did not come with predefined subscales. For such questionnaires, I undertook factor analysis and defined data-driven subscales. These questionnaires included the SHAPS, which decomposed into sensory, personal, and other-related types of pleasure subscales, UCLA, which decomposed into thriving, lack of connection, and basic connection subscales, and the LHS, which decomposed into perseverance, confidence, and helplessness subscales.

All statistical tests were thresholded at p=0.05 to determine significance. Multiple comparisons were not corrected for as the tests were pre-registered.

3.3 Results

Analogous factors emerge in the confirmatory dataset

A scree test suggested a seven factor solution(**??**). Six out of the seven pre-registered factors replicated in the confirmatory dataset: social thriving, obsession/compulsion, impulsivity, pleasure, sensation seeking/urgency, and depression-anxiety (Figure 3.2a). We did not, however, identify a factor resembling the social pain factor that we had found in the discovery data set analysis.

Transdiagnostic factors predict social choices

Participants' social thriving scores were correlated with the total friend requests they submitted in the task (n=783, r=0.07, p=0.04; Figure 3.3). In other words, people

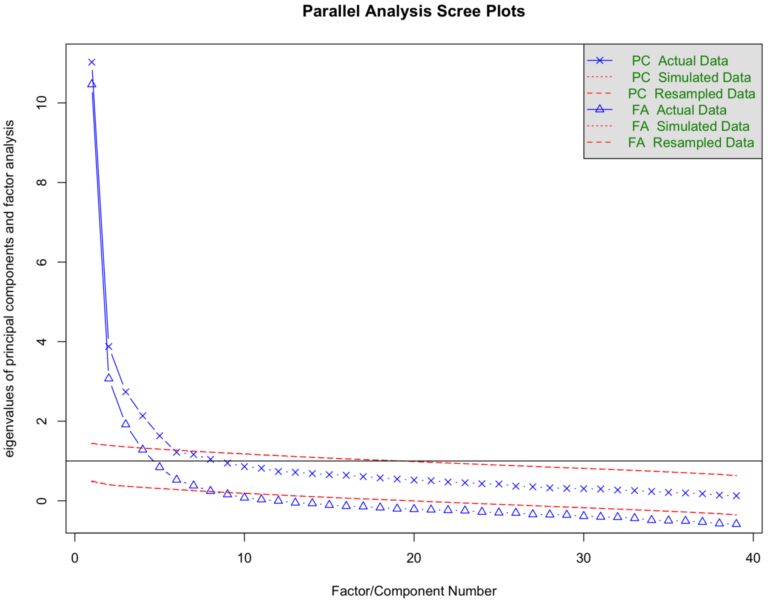


Figure 3.1: Scree plot suggests a seven factor solution

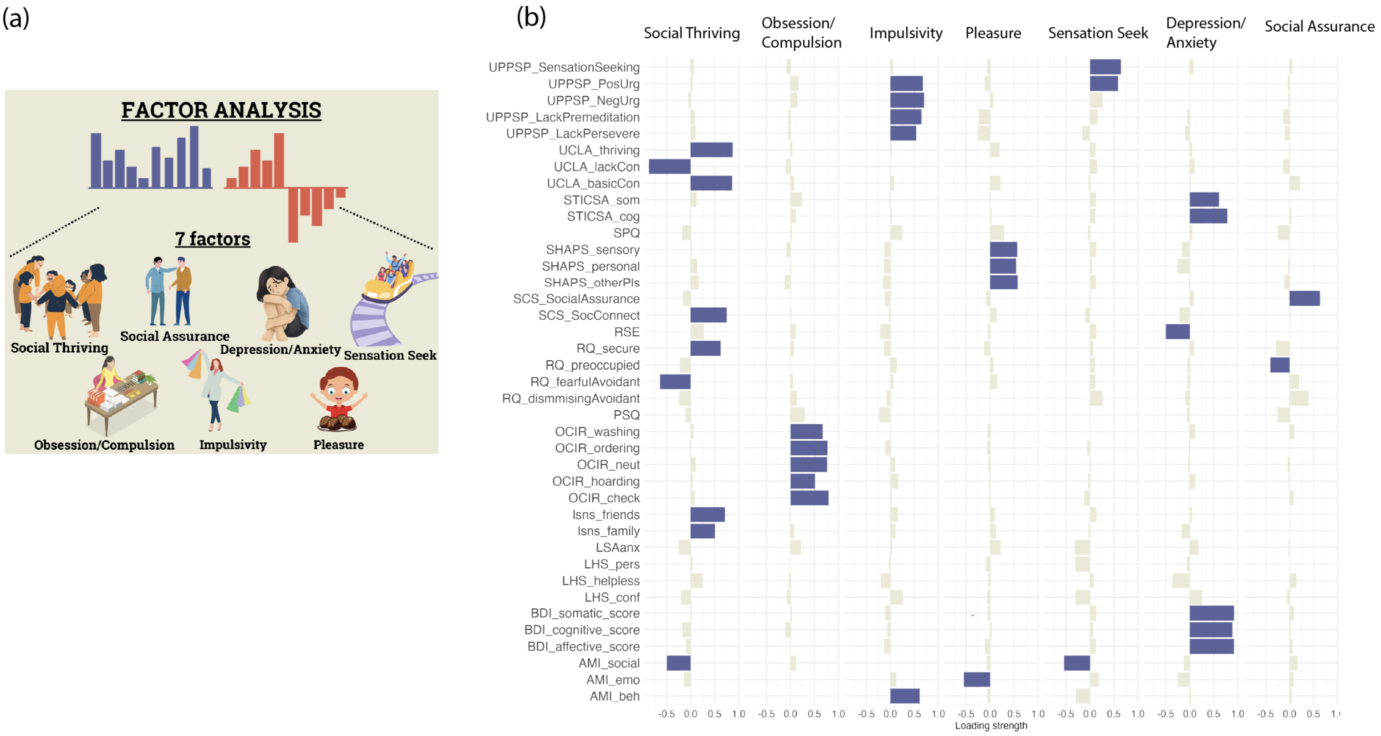
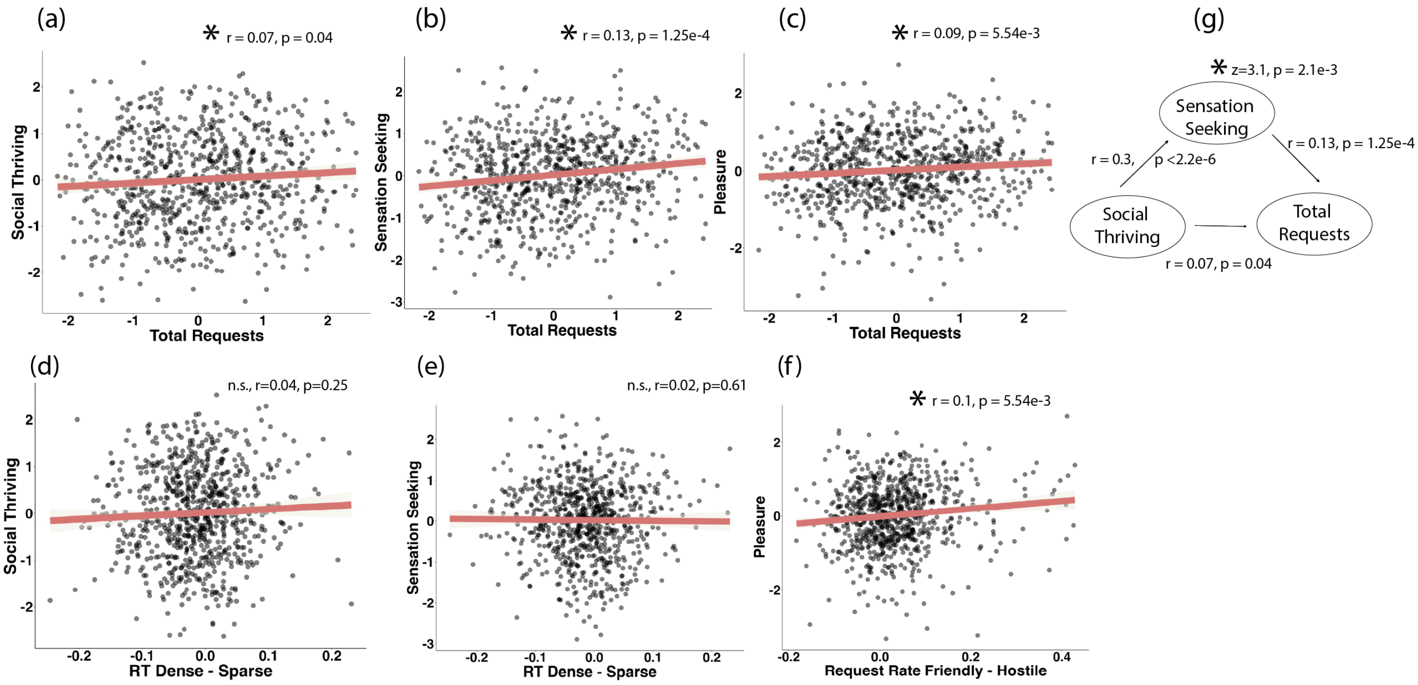


Figure 3.2: Factor structure and loadings. (a) Pictorial representations of the seven factors obtained from exploratory factor analysis (b) factor weights for all included subscales



n.s. = not significant

Figure 3.3: Relationship between social affiliation choices and trans-diagnostic mental health dimensions. (a-f) Scatter plots showing correlations between pre-registered relationships between various task measures and psychiatric factors (g) schematic showing the mediation relationship between social thriving, sensation seeking, and total friendship requests.

who more frequently requested rather than skipped a friendship opportunity were those associated with better social thriving scores. Next, participants' total requests were also related to their sensation seeking trans-diagnostic score (n=783, r=0.13, p=1.25e-4). Further, I found that the effect of total requests on social thriving was mediated by sensation seeking (n=783, z=3.1, p=2.1e-3).

Next, the total number of requests made by participants was also related to their pleasure factor score (n=783, r=0.09, p=5.54e-3). The pleasure factor was also positively correlated with impact of friendliness on the submission of friend requests (n=783, r=0.1, p=5.07e-3).

Our pre-registered hypothesis of social pain being negatively related to total requests did not replicate, because as noted above, the factor itself did not replicate.

Transdiagnostic factors do not relate to reaction times

Our reaction time-related results did not replicate. We predicted social thriving would be related to the size of the effect of density on reaction times. This, however, was not the case (n=783, r=0.04, p=0.25). Similarly, density effects on reaction times did not relate to sensation seeking (n=783, r=-0.02, p=0.61).

3.4 Discussion

In this experiment, I defined trans-diagnostic factors to create a simple yet robust profile of participant mental health and personality in a general population sample. Such definitions of mental illness challenge traditional disorder-based frameworks in favour of simple data-driven categories. Next, I showed that aspects of social decision making related to these newly derived factors.

In general, total requests sent was the most sensitive task measure, predicting psychiatric factors like social thriving, sensation seeking, and pleasure. These relationships suggest that computer based tasks are able to capture psychiatric dimensions, thereby providing external validity to the factors. The relationship between total requests and social thriving was mediated by sensation seeking, suggesting forming friendships might be part of a larger drive to accumulate sensations or experiences. Thinking of social affiliation as part of a larger drive is consistent with results suggesting hunger for food and hunger for social contact might have shared representations in the brain (Tomova et al., 2020), and that social animals like macaques consistently trade juice rewards in exchange for the opportunity to gaze at other monkeys (Deaner et al., 2005).

People's sensitivity to the friendliness of their social environments also predicted the psychiatric factor of pleasure; people who had a higher capacity to experience pleasure were also more sensitive to friendliness. Notably, the pleasure factor included loadings from the apathy motivation index. Given theoretical models linking apathy to the dopaminergic system (Nair et al., 2021; Niv et al., 2007), the pleasure-friendliness link might suggest that background friendliness might be encoded in midbrain dopaminergic areas like the SN/VTA. The next chapter will shed light on whether this prediction holds true.

A factor analysis revealed seven factors, one of which was social thriving. Typically, apart from a few diorders like social anxiety, social dysfunction is considered a symptom of other mental health disorders. The fact that social thriving emerged as a separate factor suggests that social dysfunction might be better considered a separate class of a mental health challenge. Future studies could investigate the neural underpinnings of social thriving to determine whether this factor is associated with distinct neural or functional processes.

The approach of machine learning based classification of mental health disorders has its limitations. A major strength of traditional mental health classification is that they enable comparisons between studies, thus creating a coherent literature for any given illness. Trans-diagnostic approaches may not carry this advantage, as factors that emerge from a dataset depend on the input items provided. Given the large range of diagnostic inventories, two studies with different set of input items will likely lead to different factor structures. As different studies use questionnaires relevant to their own research question, new or overlapping factors might emerge in each factor based solution, thus making it hard to create a coherent narrative around psychiatric illness.

Given similar inputs, factor structures should however, replicate over time. This means that future studies need to strike a balance between using previously known factors and being agnostic to the latent factors of their own dataset. This will enable comparison across studies and lead to a coherent literature, while at the same time iteratively defining new categories to correspond better to clinical symptoms and neurological markers.

The factors emerging from machine learning based approaches not only redraw mental illness' boundaries, but they may also reframe questions in psychiatry in more profound ways (Gillan and Seow, 2020). So far, psychiatry has been using symptoms as the "ground truth" for assigning diagnoses and formulating treatments.Trans-diagnostic approaches move away from these subjective unreliable symptom clusters and instead use the power of big data to create a more robust and replicable "ground truth". These newer dimensions could then be used to probe brain mechanisms with the hope of finding equally robust and distinct neural dimensions tied to psychiatric conditions.

But — what about data quality? Granted, diagnoses made by clinicians carry the risk of poor inter-rater reliability, but are they still not superior to data collected through the black-box of the web? Likewise, are qualified researchers not able to administer cognitive tasks better in person than trusting their applications to do so through a web browser? Thankfully, studies using online cognitive data have produced results that mirror those of studies performed in the lab (Gillan et al., 2016). For instance, Crump et al. (2013) replicated findings from classic lab-based psychological studies like Stroop, Flanker, and priming using web-based platforms.

Instructions can also be standardised and there is no risk of variability which is otherwise inherent in verbal administration of instructions. Increased anonymity online can be also be an advantage, potentially reducing participants' incentives to lie in what might be awkward social situations for experiment conducted in-person. Similarly, demand characteristics—subtle hints coming off researchers that signal experimental aims to participants—will likely be minimised in web-based testing as participants don't see a researcher before, during, or after the experiment.

Data collected online, though, is noticeably noisier. This can be evidenced by the high attrition rate (around 30%) in my discovery and confirmatory datasets. Gillan et al. (2016) posits that the noise is largely a result of a lack of environmental control. Participants have little to no checks on what they can do during the experiments. As a result, people might complete studies while listening to music, multi-tasking on Youtube, or while talking to someone else. Indeed, Ramsey et al. (2016) showed that participants recruited online were less likely to read instructions than those in the lab. However, large sample sizes and carefully constructed data quality checks should offset this problem, but care must be taken to account for systematic sources of bias (for e.g. studies of addiction might recruit populations that are more likely to be intoxicated while doing the study).

Finally, psychiatric data collected online is not only able to afford standardisation, but also generalisation (Gillan et al., 2016). Web based data is often demographically representative of populations, and if not so automatically, can be manually made to be so. It also transgresses geographical boundaries enabling people who normally do not live in proximity to research institutions to participate. Finally, it also makes access to special sections of populations easier.

The benefits of web-based psychiatric data, however, should not deter researchers from understanding subjective experience. At the end of the day, psychiatry seeks to help people seeking relief from symptoms. However, trans-diagnostic approaches could then bridge clinical presentation of symptoms to their treatment in a fashion that is more robust than the current approach of disorder-based diagnoses. Before that were to happen, more research is needed on how trans-diagnostic factors would relate to behaviours, neural circuits, and treatment outcomes.

3.5 Conclusion

In this chapter, I investigated the relationship between social decision-making in changing environments and one's psychiatric and mental health profile. Participants completed a social decision-making task and answered a series of questions about their mental health and personality. A factor analysis revealed a 7-factor solution that encapsulated shared variance across multiple questionnaires. Next, some of these factors (e.g. social thriving) were related to task behaviour (e.g. total requests submitted). Finally, I discussed some advantages and disadvantages of using machine learning based trans-diagnostic approaches to categorise mental health conditions.

In the next chapter, I will investigate the neural mechanisms of social affiliation decisions in environments that differ in the background friendliness and density levels.

Chapter 4

Neural mechanisms of social affiliation choices in different environments

4.1 Introduction

Thus far, I have shown that the background statistics of the environment affect our decisions to initiate social affiliation. However, the neural mechanisms of such decisions, i.e. how the brain integrates information about social contexts, remains unknown. Based on past studies, I hypothesise that a cortico-subcortical circuit might represent the background statistics of social environments (Priestley et al., 2024; Trier et al., 2023a; Wittmann et al., 2020). In particular, five subcortical regions—the dorsal raphe nucleus (DRN), the lateral habenula (Hb), the substantia nigra (SN), the ventral tegmental area (VTA), and the hypothalamus—coupled with their connections to cortical areas like the anterior insula (aI) and dorsomedial prefrontal cortex (dmPFC) might encode social contexts.

In some models of animal foraging, Niv et al. (2007) have argued that opportunity costs associated with the average rate of gustatory rewards in rats should be tracked by tonic dopamine in SN and VTA. In macaque monkeys, Wittmann et al. (2020) found that the average reward rate influenced choices and was represented in the activity of the DRN, aI, and dmPFC. Similarly, Priestley et al. (2024) showed that DRN activity in macaque monkeys track transitions between rich and poor environments, and disrupting DRN activity through transcranial ultrasound stimulation reduced animals' sensitivity to environmental reward. The researchers also suggested that, together with the Hb and aI, the DRN might reconcile animals' behaviour with their foraging environment, leading them to forage more when rewards were more available and vice versa. In humans, Trier et al. (2023b) showed that distributed activity patterns spanning the DRN, Hb, ACC, and aI represented behavioural states in which people either responded to reward and foraged or responded to the potential for threat by making checking responses. Despite their differences, the tasks from all these studies shared a requirement for participants to adjust the nature and frequency of their reward-motivated behaviours so that they balance the potential rewards against the threats in the environment.

I expect decisions in social contexts might operate in an analogous manner to animal and human decisions in ecological foraging contexts. Therefore, I expect a similar network of subcortical nuclei involving the DRN, Hb, SN, and VTA to be active in representing social contexts. Given projections between these nuclei and regions like the hypothalamus, aI, and the dmPFC, I expect these regions would form the rest of the cortico-subcortical circuit that would track social contexts. Therefore, the following regions were selected as regions of interest that might encode environmental variables of friendliness and density at the time of social affiliation choices: DRN, Hb, SN, VTA, hypothalamus, aI, and the dmPFC area 9.

Finally, we know that reward processing is encoded in dopaminergic circuits originating in the midbrain areas of SN/VTA (Luo et al., 2015). Tomova et al. (2020) also suggested that social rewards were processed in dopaminergic midbrain in a manner similar to gustatory rewards. Further, (Priestley et al., 2024) showed that VTA-aI connectivity represented richness of an animals environment after pursuing rewards. Since in the present task, the friendliness of an environment directly manipulates the probability of reward, we expect that a cortico-subcortical circuit involving SN/VTA and aI to encode the friendliness of an environment at the time of outcome.

4.2 Methods

Participants

A total of 26 (mean age = 24.4, males = 10, females = 16) participants met the final inclusion and exclusion criteria.

Participants had to meet the following inclusion criteria:

- Willing and able to give informed consent
- Right-handed
- Age 18 to 40 years
- Normal or corrected to normal vision
- Fluent in English
- Safe to scan at 7T (established using a checklist provided by the Wellcome Centre for Integrative Neuroimaging - WIN)

After acquisition, participant data was also excluded on the following basis:

- Request rate was 0 (no requests sent) or 1 (only requests sent) for 2 or more blocks, indicating inattention to task instructions
- Maximum standard deviation of request rates was greater than 0.3, indicating noisy behaviour

Here is the table of excluded participants by criteria:

Exclusion criteria	Number excluded
Multiple blocks with only requests or skips	3
Inconsistent request rates	1

Procedure

The study was approved by the Medical Sciences Division Interdivisional Research Ethics Committee (Ethics Approval Reference: R77443/RE002). A total of 30 participants were recruited from the Oxford area using Oxford Participant Recruitment system and other online and email-based advertisement platforms. Prior to attending the scan, participants were screened on the telephone (using 7T safety checklist provided by the WIN) to ensure that they were eligible to be scanned.

Informed consent was obtained from all participants before the study commenced. Participants were then asked to read through a slideshow which presented instructions about the task and the MRI scanning environment. Participants were then asked to change into scrubs. If participants had a vision prescription, magnet safe lenses and glasses were provided. Before entering the scanning area, participants were screened by a radiographer to ascertain participants' fitness to scan.

Right before the scanning session, participants were screened for surgical or other implanted metallic devices by the radiographers at the WIN. The safety to scan with any devices identified was ascertained using established WIN procedures.

Task

The same "friend request task" was used as described in the previous two chapters, albeit with some modifications to suit features of the haemodynamic response function. First, an additional jittered delay (sampled from a gamma distribution centred at 3s) was added between the response and the outcome to allow for the haemodynamic response to peak following neural activity. Next, the block duration was increased from 2.5 minutes to 3 minutes to compensate the trials lost after adding the aforementioned delay (see Figure 4.1).

Participants indicated their responses by using a button box. The first button was used to send a friend request, the second key was used to skip sending a friend request. This button box was placed in the right hand of the participants as they lay inside the scanner.

MRI protocol

Scans were performed on a 7T Siemens scanner. A structural scan was obtained using isometric voxels sized 0.7 mm. A total of 256 slices were obtained using the GeneRalized Autocalibrating Partial Parallel Acquisition (GRAPPA) acceleration mode with an acceleration factor of 2. The phase encoding direction was anterior to posterior, and the slices were obtained along the sagittal plane. The repetition time (TR) was 2.2 ms and the echo time (TE) was 3.02 ms. Total duration of the structural scan was approximately 6 minutes 30 seconds.

After the structural scans were completed, field-map images were acquired using isometric voxels sized 2 mm. A total of 73 slices were acquired with an anterior to posterior phase encoding direction. The TR was 620 ms, TE-1 was 4.08 ms, and TE-2 was 5.1 ms. The slices were oriented at a -30 degree angle. Total time to acquire fieldmap images was approximately 2 minutes.

Functional scans were then collected using isometric voxels sized 1.5 mm. A multiband sequence was used to obtain a total of 74 slices, with a multiband acceleration factor of 2. The GRAPPA acceleration mode was used with an acceleration factor of 2. The slices were obtained in anterior to posterior phase encoding direction. The slices were oriented at a -30 degree angle. The TR was 2.033 s, and the TE was 18.4 ms. The functional scan lasted for approximately 50 minutes.

Respiration and electrocardiogram data were acquired while the participants lay in the scanner using instruments manufactured by BIOPAC systems. The total session duration, including set up time, was approximately 75 minutes.

Analysis

Behavioural results were analysed and figures were plotted using R v4.3.3 (R Core Team, 2024) running on RStudio v2023.12 (RStudio Team, 2020). All binary categorical variables were coded as -1 and 1. Reaction times were log transformed. Significance threshold for all tests were set at $p=0.05$.

Similar to the online task, a 2 x 2 repeated measured analysis of variance (ANOVA) was used to examine the effect of friendliness and density on request rates and reaction times. Trials were further split by request and skip trials, and a 2x2x2 ANOVA was used to measure the effect of friendliness, density, and action on reaction times.

MRI results were analysed using the FMRIB software library (FSL) (Jenkinson et al., 2012). Results were analysed using the Python programming language (Van Rossum and Drake, 2009) using the package fslpy to interface with FSL (McCarthy et al., 2024). Methods used to plot figures and make statistical inferences were the same as those used in the previous two studies.

Images were prepared by first converting functional runs from dicom file format to nifti and then reorienting them to standard orientation. Structural images were bias corrected using FSL's anatomical preprocessing script fsl_anat. Brain extraction was performed using SynthStrip (Hoopes et al., 2022).

Images were preprocessed by applying motion correction using FMRIB's Linear Image Registration Tool (FLIRT) (Jenkinson et al., 2002). Fieldmap unwarping was performed using a spatial smoothing parameter set at 3mm of full width half maximum (FWHM). Highpass temporal filtering was also applied. Functional images were registered from their native space to structural space using FMRIB's Linear Image Registration Tool (FLIRT), and further registered to standard space using FMRIB's Nonlinear Image Registration Tool (FNIRT) (Anderson et al., 2010). The Montreal Neurological Institute (MNI) 152 image in 1mm resolution was used as a standard brain template.

After the data was preprocessed, a General Linear Model (GLM) based analysis was run using FMRI Expert Analysis Tool (FEAT v6) (Woolrich et al., 2001). A double gamma haemodynamic response function was used to predict Blood Oxygen Level Dependent (BOLD) response from task based events (Lindquist et al., 2009). The following task based regressors were used in the GLM.

- Face onsets friendly dense (FD)
- Friendliness FD (parametric)
- Density FD (parametric)
- Action (requests or skips) FD (parametric) . . . and so on, for all the remaining block types, namely friendly-sparse, hostile-dense, and hostile-sparse. All parametric effects were z-scored.

In addition, motion and noise based regressors were included in the GLM. Physiological noise correction was performed using physiological noise modelling (PNM) tool, part of the FSL package (Brooks et al., 2008).

The parameter estimates from the fitted model were then extracted for predefined regions of interest (ROI). For all ROIs but the DRN, masks were obtained from similar previous studies (Trier et al., 2023b) and standard atlases (Pauli et al., 2018). The DRN mask was drawn by eye using the standard diffusion template included as part of FSL. The rationale for using a diffusion template was the finding that the DRN had lower fractional anisotropy (FA) values and the surrounding tissues have higher FA values, thus leading to an identifiable dark spot in diffusion based FA images (Bianciardi et al., 2015).

A linear mixed-model was used to evaluate the effect of friendliness and density on brain activations in seven predefined regions of interest. The mixed-model included friendliness, density, action, region, and their interactions as fixed effects, and friendliness, density, action, and their interactions as random effects that varied with different subjects. In the event that the model failed to converge, or exhibited a singular fit, interaction terms were removed from the random effects structure.

The significance of the fixed effects and their interactions was evaluated using a mixed-model ANOVA implementing type II Wald Chi-square tests.

Among the regions that showed the density effect, we tested whether the neural effect was related to the behavioural effect using a Pearson's correlation. We then tested whether these density effects were global contextual effects, or simply a representation of the previous trial inter-trial interval (ITI). To test for global effects above and beyond previous trial ITIs, we ran the following GLM.

- Face Onsets
- Action (parametric)
- Density (parametric)
- Friendliness (parametric)
- Past trial ITI (parametric)

All parametric effects were z-scored. A linear mixed model was used on the parameter estimates to test for the effect of density (against zero). Region was included as a fixed effect, and a random intercept was included to account for variability between subjects. A t-test using Satterthwaite's method was be used to assess statistical significance of fixed effects. A mixed model ANOVA was used to determine whether the parameters estimates for density and past trial ITI differed from each other.

Finally, a psychophysiological interactions (PPI) analysis was performed, seeded at the DRN, to test for changes in functional connectivity between DRN and aI as a function of density. For the PPI analysis, data processing was carried out using FEAT (FMRI Expert Analysis Tool) Version 6.00, part of FSL (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl). Parameter estimates were thene extracted from the aI. A Pearson's correlation was used to determine whether the strength of the PPI estimates were related to the behavioural effect of density.

A similar PPI analysis was performed seeded at the SN to test for functional connectivity with the aI that co-varied as a function of the interaction between friendliness and outcome. Parameter estimates, extracted from the aI, were then tested against zero using a t-test.

4.3 Results

Environmental friendliness and ITI based density influences social affiliation choices

A 2x2 ANOVA showed a significant effect of friendliness on request rates (df=25. F=7.30, p=0.012, $\eta_p^2 = 0.226$; Figure 4.1a). People were more likely to send a friend request in friendly environments compared to hostile environments. While there was no effect of density when accounting for all trials, exclusion of the first 10 trials in each block to allow for an initial learning of ITI distributions revealed an interaction between friendliness and density (df=25, F=4.985, p=0.035, $\eta_p^2 = 0.166$; Figure 4.1b), similar to the analysis performed in online study in chapter two[1].

Environmental friendliness interacts with participant action to influence reaction times in social choices

A 2x2x2 ANOVA showed an interaction between friendliness and action on reaction times (df=25, F=6.836, p=0.015, $\eta_p^2 = 0.215$; Figure 4.1d). People were faster to skip than to send a request, but this was especially the case in friendly blocks.

Regions of interest encode a global density effect

A mixed-model ANOVA showed a main effect of density across regions of interest (Figure 4.2a). Sparser blocks showed higher activation than denser blocks (df =1, χ^2=6.34, p=1.17e-2). There was also a density by region interaction (df=6, χ^2=14.17, p= 2.77e-2).

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[1] a-behavioural-assay-of-social-affiliation-decisions

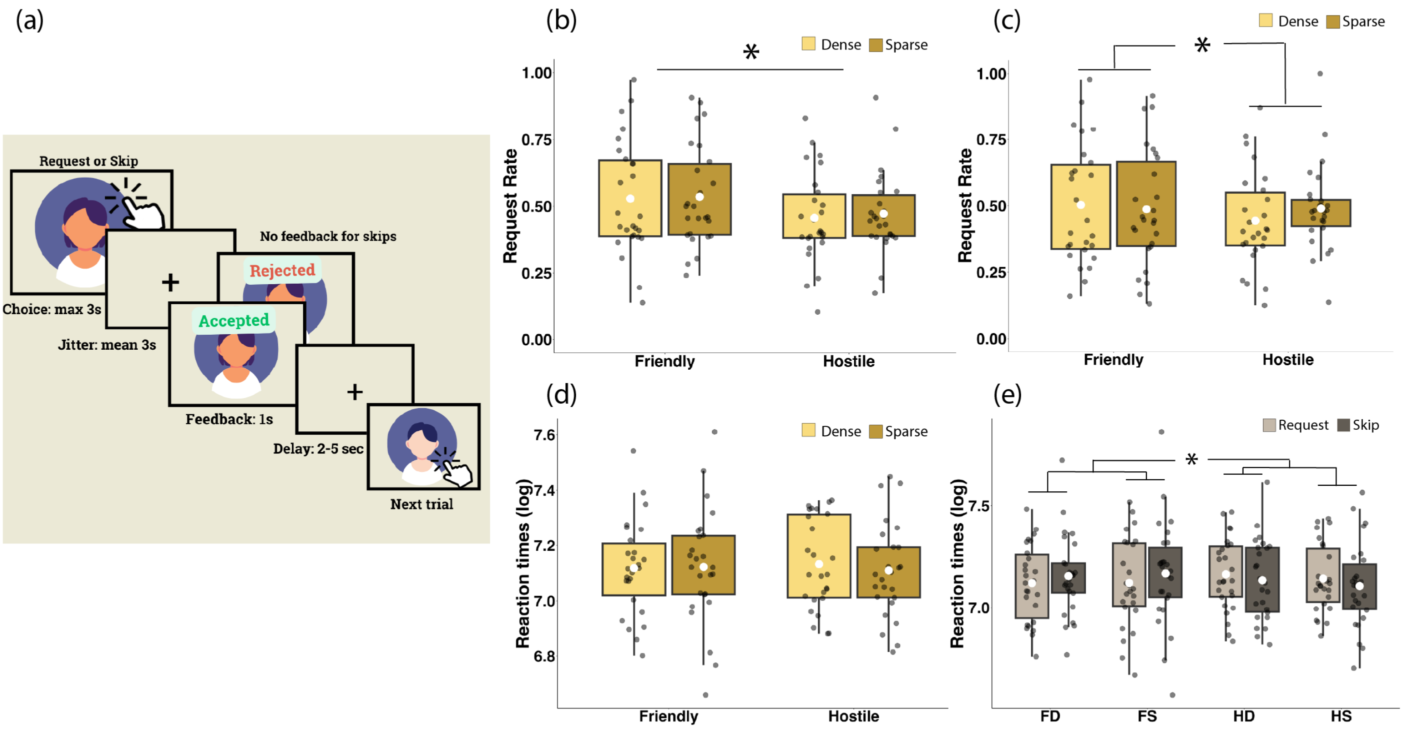

Figure 4.1: Behavioural results. (a) Schematic representation of the friend request task with timings modified to suit the features of the BOLD signal (b) effect of background environment on request rates in all trials. Request rates were higher in friendly blocks. Y-axis represents request rates, x-axis represents friendliness levels, and colour represents density levels (c) effect of background environments on all but the first 10 trials in each block. Request rates were higher in friendly and sparse blocks. (d) effect of background environments on reaction times. Y-axis represents log-transformed reaction times (e) effect of environments on reaction times split by action type (request/skip). Reaction times were faster in friendly blocks, especially when the participant skipped sending a friend request. Y-axis represents reaction times, x-axis represents the four types of environments (FD: friendly, dense; FS: friendly, sparse; HD: hostile, dense; HS: hostile, sparse), and colour represents participant action (request/skip).

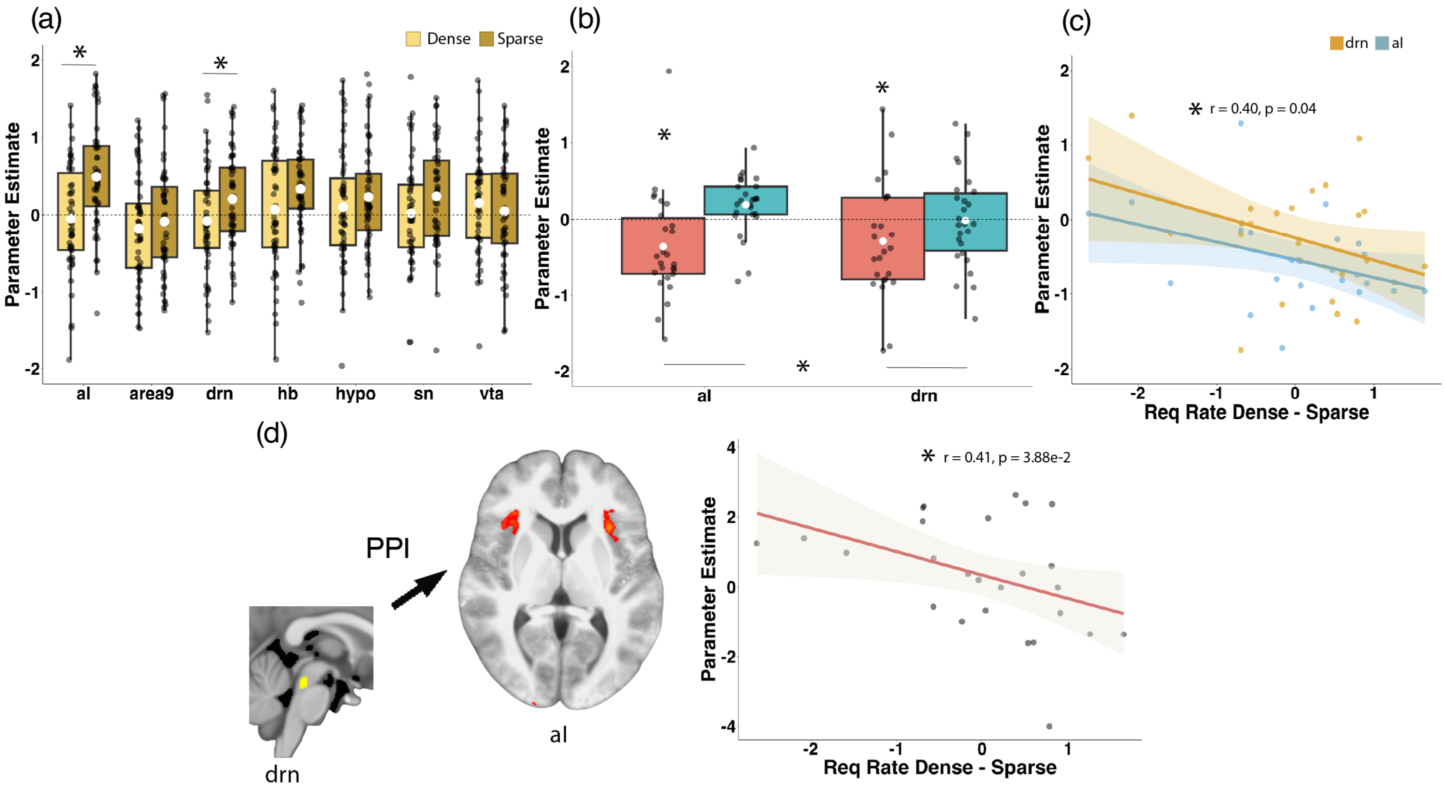

Figure 4.2: Neural effect of social density. (a) Density effect across 7 regions of interest. X-axis denotes the various regions of interest, y-axis shows scaled parameter estimates (b) density effect when controlled for past trial ITI in the aI and DRN. Colour represents explanatory variable from the GLM, namely the parametric effects of density and previous trial ITI (c) neural effect of density in the aI and DRN relates to the behavioural effect of density. X-axis represents the behavioural effect of density calculated as the difference in request rates between dense and sparse blocks. Colour represents the parameter estimates obtained from the drn and aI (d) PPI effect of density in the aI seeded at the DRN plotted against the behavioural effect of density.

Region-wise post-hoc tests were conducted to determine the nature of these interactions. A mixed model ANOVA showed a main effect of density in the DRN (df=1, χ^2=7.65, p=0.03) and aI (df=1, χ^2=20.505, p=4.1e-5) after correcting for multiple comparisons.

Given the density effect was mainly driven by the DRN and aI, we further checked whether the effect of density truly reflected the extended experience of long ITIs and thus opportunities over the duration of the block or a simply the length of the most recent interval since encountering a friend seeking opportunity. We, therefore, assessed whether an effect of density was still present in these brain regions when controlling for the most recent inter-trial interval (ITI). A linear mixed model showed that a density effect remained significant across both regions (df=25, t=-2.19, p=3.84e-2; Figure 4.2b) even after including the most recent past ITI in the GLM. Further, a mixed model ANOVA showed that the density effect was significantly different from the past trial ITI effect (df=1, χ^2=14.37, p=1.5e-4). Finally, we found that the behavioural effect of density was correlated the neural effect of density both in the aI (df=24, t=-2.13, r=0.4, p=4.34e-2; Figure 4.2c) and the DRN (df=24, t=-2.12, r=0.4, p=4.42e-2).

Density effect is represented in the DRN-aI network

A psychophysiological (PPI) analysis between the DRN and aI showed that the strength of density dependent functional connectivity correlates with the behavioural effect of density on request rates (df=24, r=-0.41, t=-2.18, p = 3.88e-2; Figure 4.2d).

Regions of interest encode an interaction between friendliness and action

A mixed model ANOVA showed an interaction between friendliness and density (df=1, χ^2=5.26, p=2.17e-2; Figure 4.3a-b). There was also an interaction between friendliness and action (df=1, χ^2=10.73, p=1.05e-3), and a triple interaction between friendliness, density, and action (df=1, χ^2=6.15, p=1.31e-2). The main effect of

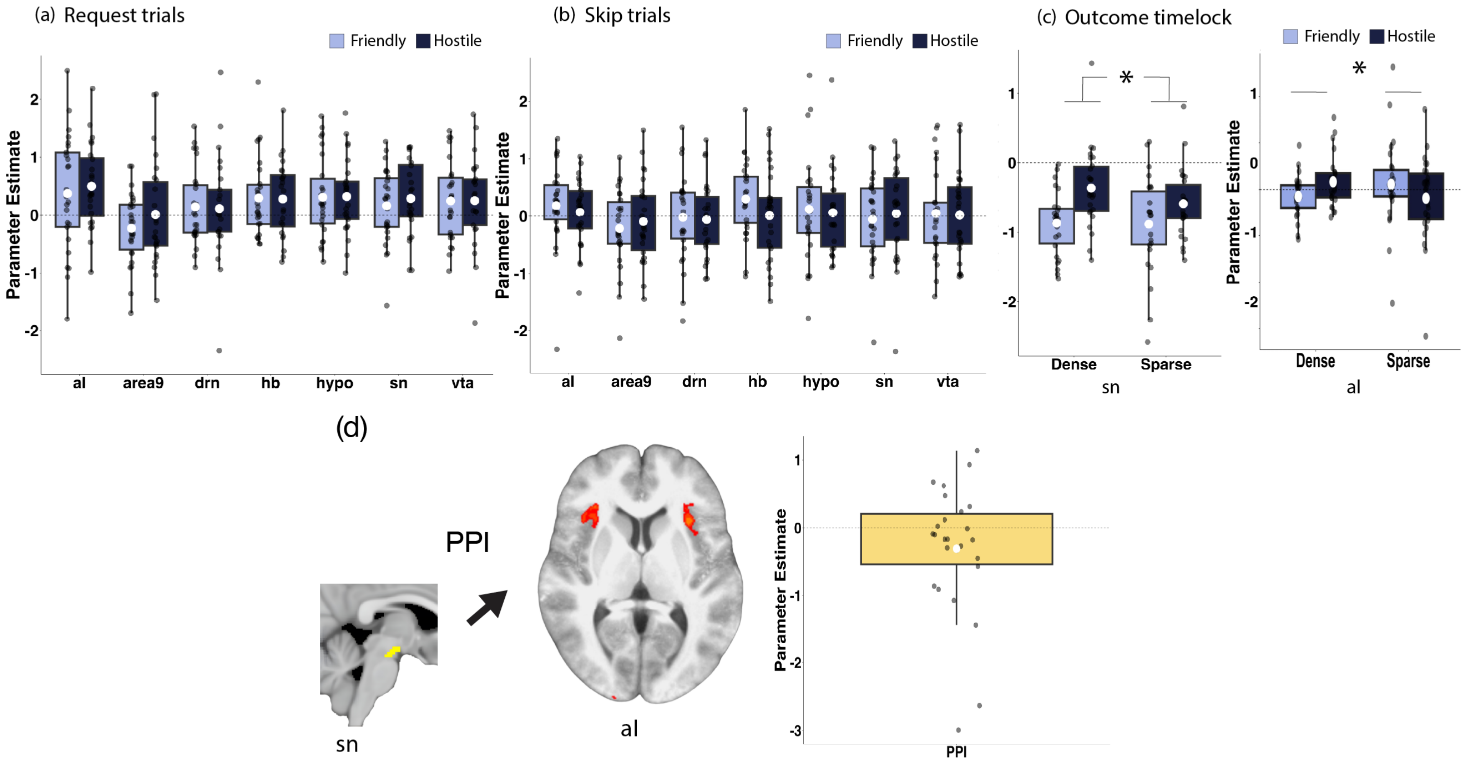

Figure 4.3: Neural effect of environmental friendliness. (a-b) Friendliness effect on regions of interest separated by request and skip trials, at the time of face onset. X-axis represents the various regions of interest, y-axis represents scaled parameter estimates, and colour represents the levels of friendliness. (c) friendliness effect in the SN and aI on parametric variable of outcome, at the time of the outcome. The interaction between friendliness and density has a significant effect on the parametric effect of outcome. X-axis represents density levels. (d) PPI effect in the aI seeded at the SN as a function of the interaction between friendliness and action.

friendliness was stronger in request trials; in other words, BOLD activity differed between friendly and hostile blocks, but it did more so in request trials. Finally, the interaction between friendliness and density was stronger in skip trials. In other words, BOLD activity differed with the interaction between friendliness and density, but did more so in skip trials.

Friendliness and outcome interaction is encoded in the SN and aI

A linear mixed model showed an interaction between friendliness and density on the parametric effect of outcome at the time of outcome in the SN but not in the VTA (df=1, χ^2=4.38, p=3.65e-2; Figure 4.3c). There was also a main effect of friendliness on outcome in the aI (df=1, χ^2=7.60, p=5.82e-3). In other words, BOLD activity representing the parametric effect of outcome varied as a function of friendliness in the aI.

Friendliness effect might be represented in the SN-aI network

A PPI analysis suggested a trend of connectivity between SN and aI that varies as a function of the interaction between friendliness and outcome (df=25, t=-1.65, p=0.10; Figure 4.3d).

4.4 Discussion

The aim of this chapter was to investigate whether social environments were represented in the brain, and if yes, how do background friendliness and density affected these representations. I found that background statistics of an environment were indeed tracked by the brain. A priori regions of interest (ROI)—namely the DRN, area 9, aI, Hb, hypothalamus, SN, VTA—encoded the density effect; that is, the activity in these ROIs reflected how often opportunities for affiliation arose. Further, this effect was present despite controlling for past trial ITI, and was strongest in the DRN and the aI. Indeed, a PPI analysis showed that the DRN and insula connectivity varied as a function of both the neural and behavioural effect of density.

The DRN is a key nucleus producing serotonin in the brain, and it maintains reciprocal connections with the aI. Given the involvement of the DRN-aI connectivity in representing density, it likely that a serotonergic system is involved in representing density in the brain. This result is in line with previous studies that showed that the DRN tracked background reward rates in macaque monkeys Priestley et al. (2024); Wittmann et al. (2020), and also in humans (Trier et al., 2023a).

The DRN, while primarily known for being a serotonin nucleus, also has other types of neurons. Hence, to test whether the relationship between DRN-aI connectivity and density is mediated by serotonin neurons, future studies could manipulate the levels of serotonin using drugs like sertraline, a selective serotonin re-uptake inhibitor. Such a causal manipulation will clarify whether the density representation in the DRN-aI network is predominantly driven by serotonergic neurons.

We also observed an interaction between friendliness and action. The friendliness effect on brain activation was stronger in request trials than in skip trials. Further, the SN showed a friendliness and density interaction on the effect of outcome, and the aI showed a main effect of friendliness. We further found a trend suggesting functional connectivity between the SN and aI that covaried with the interaction of friendliness and outcome.

Given the well-known role of dopaminergic neurons in reward processing (Luo et al., 2015) and action initiation (Khalighinejad et al., 2020), it is likely that a dopaminergic system is responsible for tracking environmental friendliness in the present experiment. This is consistent with the view that social rewards might be represented in a similar manner in the brain as monetary or gustatory rewards (Keramati and Gutkin, 2014). However, a direct manipulation of dopamine levels, for instance using a dopamine antagonist like clozapine, will be needed to ascertain the role of dopaminergic neurons in tracking the friendliness of environments.

Finally, a key region that represented both friendliness and density was the aI. The aI also showed functional connectivity with the DRN as a function of density, and a trend for connectivity with the SN as a function of the interaction between friendliness and outcome. While claims of directionality in such cases are hard to make, various studies have observed the aI as a central hub of cortico-subcortical circuits representing environmental variables (Khalighinejad et al., 2020; Priestley et al., 2024; Trier et al., 2023a). It is possible that the cortical aI integrates information about the environment and sends projections to various subcortical areas, which further co-ordinates brain-wide activity and ultimately, behavior; in other words, the aI could be acting as an integrative hub. A hypothesis that follows from this aI-as-an-integrative-hub theory is that lesioning the aI or adding noise to its activity, for instance through non-invasive trans-cranial ultrasound stimulation, would lead to the disruption of circuits tracking both environmental friendliness and density. A future study could examine this hypothesis.

4.5 Conclusion

In this chapter, I examined the neural correlates of environmental friendliness and density in a social affiliation task. Analysis across predefined regions of interest—namely the DRN, aI, Hb, area 9, hypothalamus, SN, VTA— showed a network wide effect of density and an interaction of friendliness and action at the time of face onsets. The density effect in the DRN and aI was present even after controlling for past trial ITI, and a PPI analysis showed the DRN-aI connectivity strength scaled as a function of the neural and behavioural effect of density. Consistent with its role in reward processing, the SN showed a friendliness density interaction on outcome whereas the aI showed a main effect of friendliness on outcome. Finally, the connectivity between SN-aI showed a trend of varying with the interaction between friendliness and outcome.

Chapter 5

Linking neural markers to psychiatric factors

5.1 Introduction

So far, we have seen that global contexts of friendliness and social density affect affiliation choices. We have also seen that subcortical nuclei like the dorsal raphe nucleus (DRN) and the substantia nigra (SN) might be involved in representing such contexts in the brain. In this study, I aim to bridge the psychiatric results and the neural results and answer the question: what neural markers could relate to trans-diagnostic psychiatric dimensions?

In an ideal world, answering this question would mean computing trans-diagnostic psychiatric factors for participants in the MRI study. However, for such a study to be well powered, it will require fMRI and psychiatric data from hundreds of participants. This feat of data collection would be time consuming and unaffordable. More generally, such practicalities preclude investigations of neural effects that are expected to be of small magnitudes. To meet this need for large MRI datasets, projects like the Human Connectome Project (HCP) have been undertaken, which aim to create a large dataset of preprocessed MRI scans which can be accessed by researchers internationally to help them address the issues that they are investigating.

The HCP consortium is a collaborative project led by researchers from Washington University, University of Minnesota, and the University of Oxford (Van Essen et al., 2013). Its aim is to map human brain circuits and their relationship to behaviour in large populations. The HCP dataset includes task-based, resting state, and diffusion-MRI data from over 1000 participants, along with performance measures in various cognitive tasks and responses to various psychiatric questionnaires.

While the HCP dataset solves the problem of power, the questions linking brain and behaviour that it can be used to answer remain limited to those that are linked to the behavioural measures already acquired as part of the HCP protocol. For instance, while the HCP dataset does include some psychiatric and personality questionnaires, they tend to be limited in number and not tailored for deriving task-specific or domain-specific trans-diagnostic factors. For the purposes of the present study, I cannot derive factors corresponding to social thriving or pleasure from the friend request studies, and consequently cannot further link them to any neural markers.

Luckily, recent advancements in machine learning have dramatically increased the predictive accuracy of models. For instance, a deep neural network could be used to train and classify images of numbers with predictive accuracy as high as 99% (Nielsen, 2015). In my case, such algorithms could be trained to predict trans-diagnostic scores using the limited set of shared questionnaires completed by participants both in the online dataset and in the HCP dataset.

In the present study, I will predict trans-diagnostic factor scores for participants in the HCP dataset through computational models trained on the confirmatory dataset from the friend request study (n=783, chapter 3[1]). This prediction is possible because we included a few additional questionnaires in our online study which were also completed by participants in the HCP dataset. Having obtained factors for the HCP dataset that are related to psychiatric dimensions identified in chapter 3, I will then test whether these psychiatric dimensions are related to resting state connectivity between specific regions of interest.

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[1] relationships-between-mental-health-and-personality-profiles-and-the-

Which factors might be related to resting state connectivity, and between which regions? In chapter 3[2], we observed and replicated a correlation between the friendliness effect on request rate and a person's trans-diagnostic factor score corresponding to the ability to experience pleasure. In chapter 4[3], we observed that connectivity between the SN and aI might vary with the interaction between environmental friendliness and outcome. Liking these two findings, I hypothesise that the trans-diagnostic pleasure factor might relate to resting state SN-aI functional connectivity in the HCP dataset.

Having trans-diagnostic factors for the HCP dataset is akin to having these participants complete the entire battery of questionnaires from the friend request study in chapter 3. The availability of these factors would then enable further supplementary analyses. For instance, social well-being has been associated with structural differences in the brain. Molesworth et al. (2015) found that social network diversity was associated with increased white matter volume using diffusion tensor imaging. Hyon et al. (2022) found that white matter integrity in regions supporting social and affective processing was significantly higher in individuals who occupied more central positions in social networks. Filley (2020) has argued that robust myelination along tracts supporting social cognition might confer adaptive social benefits like prompt empathic concern for offspring and prompt co-operative and altruistic behaviours. Thus, I hypothesise that the trans-diagnostic social thriving factor would relate to total white matter volume in the HCP dataset.

Finally, it is well established that social thriving is related to increased physical health, to a reduced mortality risk, and increased longevity (Cacioppo and Cacioppo, 2014b). It is also known that one of the key predictors of longevity is one's cardiovascular fitness (Strasser and Burtscher, 2018), and consequently one's endurance levels (Lanza et al., 2008). Indeed, Teramoto and Bungum (2010) showed that elite endurance athletes have a reduced mortality rate and increased longevity

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[2] relationships-between-mental-health-and-personality-profiles-and-the-

[3] neural-mechanisms-of-social-affiliation-choices-in-different-environments

compared to the general population. Therefore, I hypothesise that an individual's social thriving factor would also be related to their levels of physical endurance.

5.2 Methods

Participants

Two datasets were used in this study. First, for model evaluation and fitting, data from participants in chapter 3 were used. Participants were the same as those described in chapter 3, and they were subjected to the same inclusion and exclusion criteria. In brief, 783 participants were tested in the confirmatory dataset (mean age = 27.3, males = 392, females = 380, other = 11). Next, for testing relationship between psychiatric factors and neural features like functional connectivity, data and ethics were provided by the Human Connectome Project (https://www.humanconnectome.org; n=1206, males = 550, females = 656), WU-Minn Consortium (Principal Investigators: David Van Essen and Kamil Ugurbil; 1U54MH091657), funded by the 16 NIH Institutes and Centres that support the NIH Blueprint for Neuroscience Research; and by the McDonnell Centre for Systems Neuroscience at Washington University. All participants gave informed consent and were reimbursed for their time ($450 for 3T MRI) and travel. HCP participants were scanned at the McDonnell Centre for Systems Neuroscience at Washington University, University of Minnesota (WU-Minn), USA, on a Siemens Skyra 3 Tesla scanner.

For resting state analysis, a subset of 400 (males = 207, females = 193) datasets were obtained from the 1206 participants. These participants were obtained from the study by Klein-Flügge et al. (2022b), and were selected on the basis of the following criteria: the quality of the physiological variables acquired, and their total DSM/ASR score, to allow for maximum subclinical variance across participants. For full details on participant selection, see Supplementary Methods for the study by Klein-Flugge and colleagues. (Klein-Flügge et al., 2022b).

Task

In addition to the "friend request task" and its associated psychiatric questionnaires, we administered a few additional questionnaires. These questionnaires were selected from the questionnaires that participants from the HCP dataset had completed, thus forming a basis for the same model to be used in both datasets.

The questionnaires selected were the following:

- NIH friendship and emotional support toolboxes (Cyranowski et al., 2013).
- Ten item personality inventory (TIPI), comprising the agreeableness, openness to experience, emotional stability, extraversion, and conscientiousness sub-scales (Gosling et al., 2003).

The questionnaires were thought had the best chance (amongst questionnaires in the HCP dataset) of describing variance related to the social and non-social features of the friend request task.

Analysis

The process of model selection, fitting, and evaluation was performed using the 'tidymodels' package in R. First, questionnaire scores were scaled and centred (z-scored) across participants. Then, the dataset were split into training and testing datasets (three quarters of the data were used for training and the remaining quarter was used for testing).

Two types of candidate models were defined to predict psychiatric factor scores from shared questionnaires between the online dataset and the HCP dataset: one with a simple linear structure, and a second that included a product of the friendship and emotional toolbox scores in addition to the linear effects. Next, four types of algorithms were chosen for fitting: neural networks (nnet), simple linear regression (lm), linear regression with penalised maximum likehood (lmnet), and random forests (rf). This led to a total of 4x2=8 candidate models.

Hyperparameters for the models were tuned using the ‘tuning’ package in R, and then models were fit according to the respective algorithms listed above. Models were then compared using the root mean squared error (rsme) and r^2 metrics. Winning models selected were those that maximised r^2 and minimised rsme. Finally, the winning models were validated on the testing dataset using a Pearson’s correlation between the true and predicted values.

In the HCP neural dataset, four resting state runs were acquired on a 3T Siemens scanner (Smith et al., 2013; Van Essen et al., 2013). Each run lasted 14.4 minutes, had a repetition time (TR) of 720ms, echo time (TE) of 33ms, resolution of 2mm isotropic. A total of 72 slices were acquired with a multiband factor of 8 resulting in 1200 timepoints. These data were then corrected for distortions, temporally-filtered, minimally smoothed and projected onto a surface reconstruction obtained from aT1-weighted image (Smith et al., 2013).

While the HCP dataset is of high quality, there have been concerns about relatively weak signals in the subcortical areas. As noise caused by physiological movements (respiration, pulse, etc.) particularly affects the subcortical areas, Klein-Flügge et al. (2022b) further performed additional corrections for physiological noise. They used the PNM toolbox (https://fsl.fmrib.ox.ac.uk/fsl/docs/#/task_fmri/pnm) to generate physiological and motion regressors. Further they used Independent Component Analysis to generate further noise regressors. All motion, physiological, and noise regressors were normalised. These regressors were then used to remove motion and physiology based confounds from the dataset. The resultant data was then demeaned, the variance in noise was normalised, and all four runs were concatenated. For additional details on the aforementioned preprocessing steps, please refer to Klein-Flügge et al. (2022b).

With a full preprocessed neural dataset, time series were extracted from the SN, and the FOP4 region of the aI. Average time series were extracted using MATLAB (vR2022b) using the algorithm MIGP (Klein-Flügge et al., 2022b). All further analyses, including model predictions, computing statistics, and plotting figures, were performed using R v4.3.3 (R Core Team, 2024) running on RStudio v2023.12. The HCP behavioural dataset was prepared by z-scoring behavioural measures of interest, i.e. total white matter volume and age adjusted endurance scores.

A functional connectivity score, indexed by the Pearson's r, was obtained for all participants to indicate the strength of resting state connectivity between the SN and aI. Model predictions for social thriving and pleasure score were obtained for all participants using the winning model. Hypothesised relationships were then evaluated for statistical significance using a simple Pearson's correlation test. Significance threshold was set at $\alpha = 0.05$.

5.3 Results

Model predicted psychiatric factors relate to true values

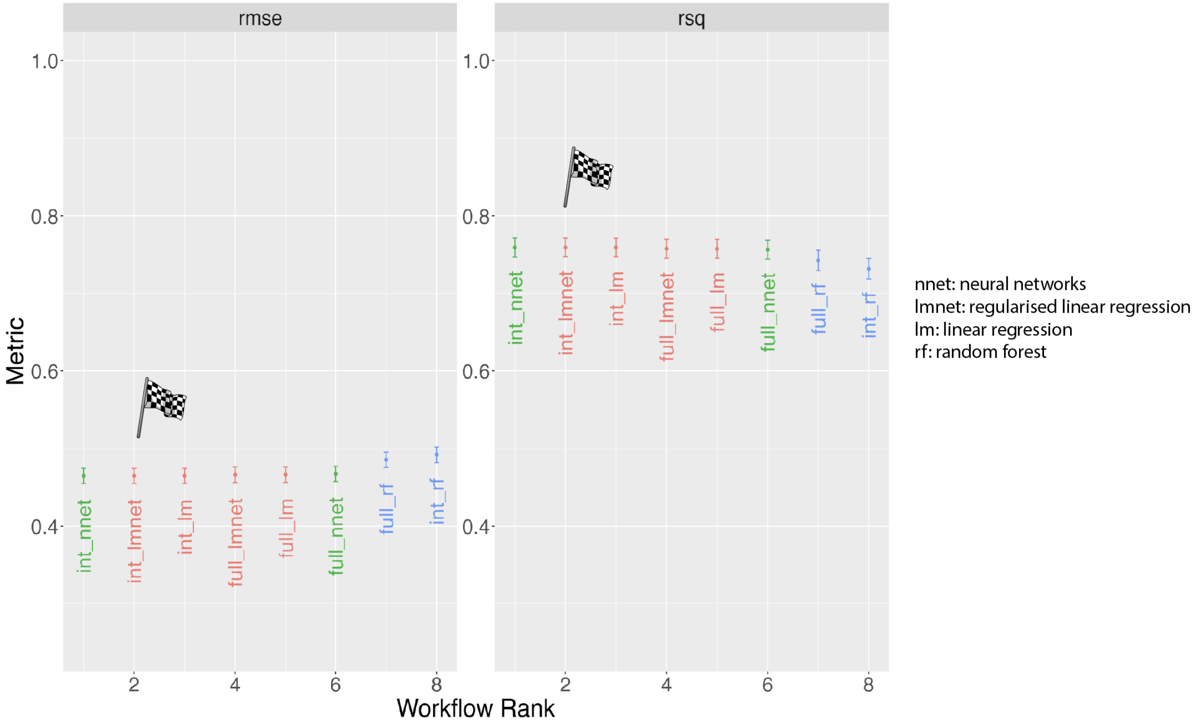

Figure 5.1: Model fits for social thriving. (a) Comparison of various model fits with winning model indicated by a race flag

The fitted models described the data well. For instance, for social thriving, among the various algorithms used to fit the model, all but random forest models led to good model fits (r^2 approximately 0.8, see Figure 5.1). Regularised linear regression models with a product term were selected as a winning model for future analysis. In the test dataset, a correlation between true and predicted social thriving values was found to be significant (df=194, r=0.90, t=25.81, p<2.2e-16, see Figure 5.2a).

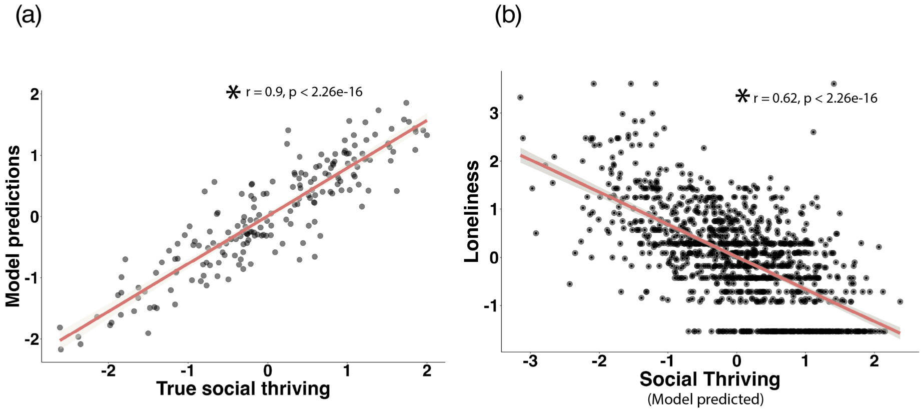

Figure 5.2: Model validation. (a) Model predicted social thriving plotted against true social thriving (b) and against loneliness scores from the HCP dataset.

As a further proof of concept, the model predicted social thriving scores were negatively correlated with loneliness scores from the HCP dataset (df=1195, t=-27.42,r=-0.62, p<2.2e-16; see Figure 5.2b).

A model with the same predictors was used to predict scores for the pleasure factor, and predicted pleasure scores were also found to be significantly correlated to true pleasure scores in the testing dataset (df=194, t=4.22, r=0.3, p=3.73e-5).

SN-aI connectivity relates to predicted pleasure factor score

Model derived pleasure scores were significantly correlated with the functional connectivity score between SN and aI, a region of the aI (df=96, r=-0.11, t=-2.34, p=1.97e-2; see Figure 5.3); the greater the connectivity between SN and aI, the lower the participant pleasure score.

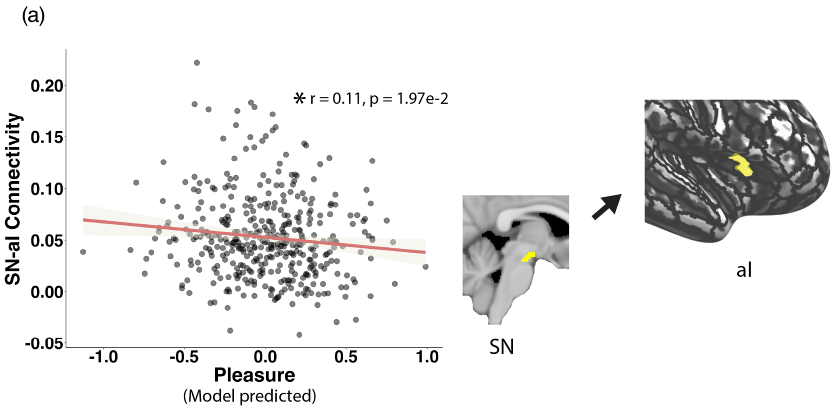

Figure 5.3: Functional connectivity between the SN and aI plotted as a function of model predicted pleasure scores.

Social thriving relates to total white matter volume in women

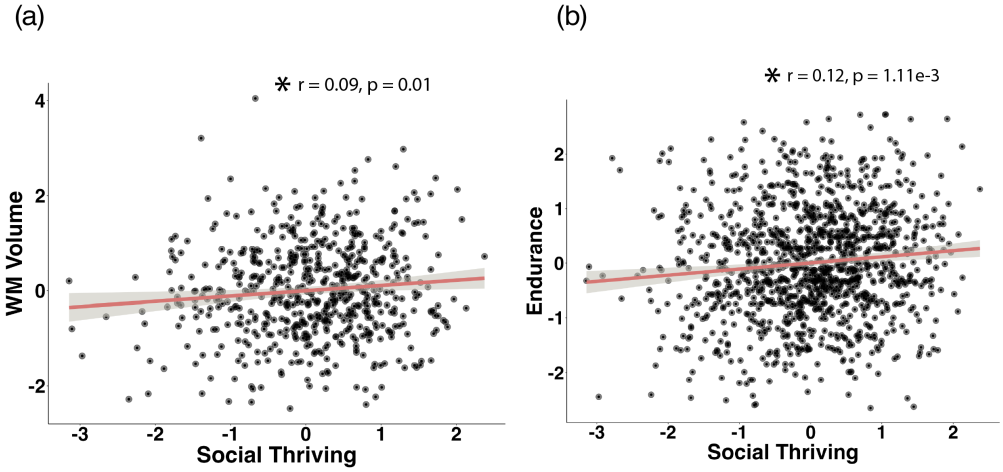

Figure 5.4: Physical and neural correlates of social thriving. (a) Model predicted social thriving plotted against total white matter volume in the brain in women (b) model predicted social thriving plotted against age adjusted endurance scores

Model derived social thriving score did not predict total whole brain white matter volume in general, but in a post-hoc test, it did predict total white matter volume in women after correcting for multiple comparisons (df=597, r=9.99e-2, t=2.451, p=0.01; see Figure 5.4). The total white matter level in women scaled as a function of their social thriving scores.

Social thriving relates to age adjusted endurance levels

Model derived social thriving scores also predicted age adjusted endurance levels (df=645, r=0.12, t=3.26, p=1.11e-3). Participants with a higher social thriving score also had higher physical endurance levels.

5.4 Discussion

In this chapter, I demonstrated a proof-of-concept for predicting trans-diagnostic factors using machine learning methods. Next, I showed that these model-predicted psychiatric factors could explain neural markers such as functional connectivity and white matter volume. I further showed that the pleasure factor was correlated with resting state functional connectivity between the SN and aI.

As described in chapter four, trans-diagnostic factors address many challenges associated with traditional diagnostic methods like poor inter-rater reliability and arbitrary distinctions between diseases sharing similar symptoms. However, the challenge with deriving trans-diagnostic factors is a requirement of a large number of subjects completing a large number of questionnaires.

The first challenge, that of collecting large sample sizes, is easier to address with online data-collection toolkits like jsPsych and recruitment platforms like Prolific. However the second challenge, that of large questionnaire items, has so far not been addressed. In research settings, participants are offered monetary compensation in exchange for their time. In clinical settings, asking patients to complete such large sets of questionnaires to derive their factor scores might be impractical.

Using machine learning models, I have showed that a condensed set of questionnaire items can be used to predict trans-diagnostic factors with high predictive accuracy. As a result, in the future, only studies that intend to derive and validate trans-diagnostic factors might need to administer a long battery of questionnaires. All other studies can administer a condensed set of questionnaires and use pre-trained models to predict factor scores, saving participant time and researcher money. More importantly, a condensed battery may even ease the translation of trans-diagnostic approaches to clinical settings.

In this study, model-derived pleasure factor scores were correlated with resting state functional connectivity between SN-aI. This further supports the link between anhedonia, a major symptom associated with depression, and the dopaminergic system (Belujon and Grace, 2017). This result is also in line with the role of dopamine neurons in general reward motivated behaviour (Morales and Margolis, 2017). It is also consistent with studies showing the involvement of both the dopaminergic system's (Walum and Young, 2018) and aI's (Rogers-Carter et al., 2018) involvement in meditating social approaching and bonding.

Model derived social thriving scores were also linked to total white matter volume in women. While not hypothesised, it is not uncommon to observe sex differences in studies of social cognition at the behavioural level (Proverbio, 2023), and at the neural level (Kiesow et al., 2020). While past studies have showed large degree of overlap in sex differences in neural structures in general (Miller et al., 2016; Ritchie et al., 2018), there might be more salient sex differences when accounting for the social brain in particular (Kiesow et al., 2020). Future studies need to disentangle the similarities and differences associated between the sexes in the social brain.

Social thriving was also related to age-adjusted endurance levels. Previous studies have consistently associated social thriving with increased longevity and reduced mortality risk (Cacioppo and Cacioppo, 2014b). Another major marker linked with longevity is cardiac fitness and one's endurance levels (Lanza et al., 2008). Therefore, it is possible that endurance levels might mediate the relationship between social thriving and longevity. In other words, people who thrive socially and have a larger network of friends might have greater incentives to move and exercise, leading to greater endurance levels and consequently live longer lives. Data collected from the ongoing HCP-Ageing project, a dataset aimed at linking changes in brain and behaviour to the ageing process, might help test this hypothesis in the future.

5.5 Conclusion

In this chapter, I developed and validated a novel method for predicting transdiagnostic factors without the need for completing a long battery of questionnaires. Model predicted pleasure score was found to be linked with participant's SN-aI functional connectivity strength. Supplementary analyses also showed a link between social thriving and total white matter volume, and age adjusted endurance levels.

In the next chapter, I will investigate how background features of the environment might affect a different kind of social decision: whether to spend time around other people and benefit from their knowledge, or to go one's own way and pursue rewards independently.

Chapter 6

A behavioural assay of social learning decisions

6.1 Introduction

Social decisions come in a number of different forms. So far, I have investigated the behavioural and neural basis of decisions to send friendship requests. In the final experimental chapter of this thesis, I turn to a different kind of social decision: whether to pursue rewards independently or to spend time around others and learn from their knowledge about rewards.

Humans, and many other animals, are social beings and co-operating with others confers many adaptive benefits. For instance, learning from other conspecifics can be essential for survival. van de Waal et al. (2013) observed that infant wild vervet monkeys preferred to eat food items that their mothers preferred, even in the presence of an equally palatable alternative. Moreover, when adult monkeys were migrated to a new environment, they switched their food preferences to match that of the resident group. Wittmann et al. (2016) showed that when in co-operative environments, humans tend to confuse their own performance with that of others, a phenomenon they termed as “self-other mergence”.

Apart from the instrumental benefits of staying in proximity to others, social connection has its own inherent benefits. We have seen in chapter 1 that social connection carries numerous physical and mental health benefits. Baumeister and Leary (1995) have argued that humans have a fundamental need to belong, and more recently Tomova et al. (2020) have showed that social rewards may share common neural circuits with gustatory rewards. In fact, macaque monkeys sacrificed juice rewards in exchange for the opportunity to view images of other high status monkeys or female perinea (Deaner et al., 2005), and there is evidence of a shared social attention circuitry between monkeys and humans (Deaner and Platt, 2003). Given this propensity to connect with others, people may show a tendency to stay with others irrespective of their foraging contexts, especially when there is no competition amongst conspecifics.

Despite its many advantages, social co-operation is not without its downsides. Staying close to a conspecific might create dependency, and the weaker animals might only get what is left over, if anything at all (Strauss et al., 2022). This might prime animals to forage for food independently rather than gain knowledge vicariously through others. Indeed, in studies investigating explore-exploit dilemmas, humans chose exploration even in the presence of rewarding alternatives (Daw et al., 2006), with specific brain regions keeping track of environmental richness (Kolling et al., 2012).

How humans strike this balance between learning from others and foraging for themselves, and how that depends on environmental factors remains poorly understood. In this study we aim to answer these questions through a novel social decision-making task.

In the present task, participants made decisions to forage for rewards independently or to stay close to another player to exploit their knowledge. Such decisions were made in various background environments, which differed from each other on the following axes: the richness of rewards (the average rate of reward availability in an environment), the competitiveness of the block (whether or not participants had to outscore their opponents for their rewards to count in their total), and the level of other players knowledge.

We hypothesised that:

- People will, in general, show a tendency to stay close to others
- People will stay further apart from each other in competitive blocks compared to neutral blocks, reflecting a need for social belonging in the absence of competition
- People will stay closer to others when the other player has better knowledge of the environment, reflecting a desire to exploit the knowledge of others
- People will stay away from each other and explore independently in rich environments compared to sparser ones, reflecting the abundance of the environment.

Finally, we will also assess how individual differences in social decisions might relate to one's psychiatric and personality profile. A battery of questionnaires will be administered before and after the task and latent factor dimensions will be extracted. We hypothesise a similar factor structure will emerge as that observed in the friend request task, with factors representing social thriving, impulsivity, sensation seeking, pleasure, social assurance, and depression anxiety.

6.2 Methods

Participants

Ethical approval for the study was granted by the University of Oxford's Medical Sciences Interdivisional Research Ethics Committee (MS IDREC; Reference R82240/ RE002).

A total of 200 participants were recruited for an exploratory dataset (mean age: 27.6 years, 101 males, 99 females) pseudo-anonymously using Prolific (prolific.co). All participants were fluent in English and had normal or corrected to normal vision. Informed consent was obtained before participants started the study.

Participants were presented with written instructions prior to the start of the task. Their comprehension was then tested using a simple 6-item questionnaire. If the participants failed to answer all 6 questions correctly, they were asked to re-read the instructions and take the test again. A maximum of 3 such retests were permitted.

Before the main task commenced, participants were given a chance to familiarise themselves with the task in a short practice block. After the practice block ended, the main task commenced.

After collecting the data, we then used the following exclusion criteria:

Exclusion criteria:

- Rewards gathered during task performance were greater than 2 standard deviations from the mean

Task

Participants completed a browser based foraging task in which they played with simulated agents taking turns to navigate a virtual forest. They were instructed that they were going to play a "fruit foraging game" with another player, and that their aim was to accumulate fruit rewards in 8 total blocks lasting 6 minutes each. The movements of their co-player, the participants were told, were taken from the movements of a previous participant who played the game.

Participants used arrow keys to navigate a grid representing a forest with hidden rewards. Participants could take a maximum of 7 steps by moving up, down, right, or left in a given turn. Both the participants and the simulated agent was granted a total of 35 turns per block. The simulated players were programmed such that they took between 2 and 4 steps in each turn, with adjacent turns being separated by 100ms.

On the foraging grid, locations of fruit trees were invisible and could be accessed by arriving at the respective square. The locations of these trees were held constant

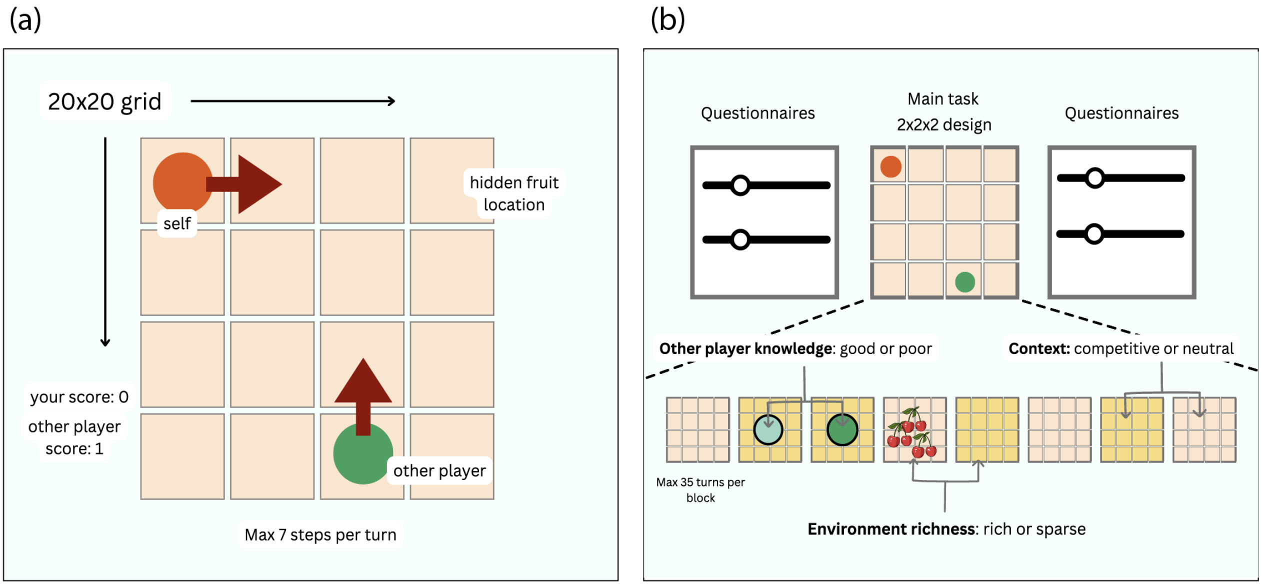

Figure 6.1: Task structure (a) schematic representation of trial structure. Participants use arrow keys to navigate a grid with hidden rewards in the presence of a computerised other player (b) schematic representation of experimental structure and manipulated factors

throughout a block and could be inferred over time. Participants were also told that they could visit locations of previously rewarding trees as the fruits would replenish.

Across the different blocks, we manipulated three independent variables. There were two levels of environmental richness: rich and poor. In rich environments, participants had to traverse a shorter distance (26 steps, versus, 53 steps in poor environments) before they encountered new fruits. This made the trees appear to grow new fruits quicker in richer environments. Next, there were two levels of other player's knowledge: high or low. While the participants were told that the movements of the other player were taken from a previous participant's data, in reality, the movements were pre-programmed. This deception was thought necessary to ensure participants' attributed social agency to the other player, and was approved by the Ethics Committee. In high knowledge blocks, it took an average of 12.25 steps for the simulated other player to find fruit, whereas in low knowledge blocks, it took an average of 21.2 turns for the other player to find fruit. And finally, there were two levels of context: competitive and neutral. In competitive contexts, participant reward was only added to their total score if it exceeded the other player's score. On the other hand, in neutral blocks, the score was added irrespective of the other player's result.

Similar to the friend request task, ten questionnaires were administered in two sets before and after the main task. The questionnaires consisted of the Snaith Hamilton Pleasure Scale (SHAPS; Snaith et al. (1995)), Social Connectedness Scale (SCS; Lee and Robbins (1995)), Learned Helpness Scale (LHS; Quinless and Nelson (1988)), Liebowitz Social Anxiety Scale (LSAS; (Liebowitz, 1987)), Autism Spectrum Quotient (AQ; Baron-Cohen et al. (2001)), Beck's Depression Inventory (BDI; Beck (1961)), UCLA Loneliness Scale (UCLA; Russel (1996)), State-Trait Inventory of Cognitive and Somatic Anxiety (STICSA; Ree et al. (2008)), Urgency, Premeditation, Perseverance, Sensation Seeking, and Positive Urgency scale (UPPSP-S; DiTommaso et al. (2004)). The following questionnaires were presented before the main task: SHAPS, SCS, LHS, LSAS, and AQ. The remaining questionnaires were presented after the task.

Analysis

Data were analysed using R (v2022) using RStudio. People's propensity to learn from others versus explore for themselves was measured by the mean change in player distance from the other player; negative changes in mean player distance meant participants sought proximity to the other player, and vice versa. A linear mixed model with the optimiser bobyqa was used to determine the effect of context (competitive or neutral frame), environmental richness, and other-player knowledge on mean change in player distance. A maximal model, that is all of the factors and their interactions, were used in the model. Satterthwaite's method was used to assess significance with threshold set at $\alpha = 0.05$.

Exploratory factor analysis was run on questionnaire subscales to extract latent dimensions. The minimal residual solution and promax rotation were used to extract the factors. Factor scores were extracted using the Thurnstone method. Finally, a Pearson's correlation was used to measure the relationship between factors and relevant task measures.

6.3 Results

People show a general preference to stay close to others

A linear mixed model showed a significant effect of the intercept (df=237, t=-20.869, p<2e-16) on change in player distance. This suggests that irrespective of context, people preferred moving closer to the other player.

Environmental context influences social learning choices

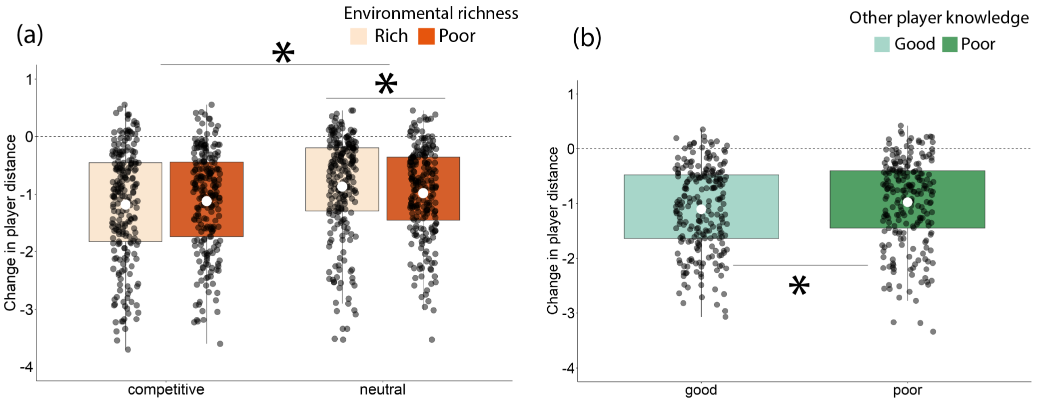

Figure 6.2: Behavioural results (a) behavioural effect of context and environmental richness on change in player distance. People were more likely to move toward the other player in a competitive context, and when the environment was reward-poor. The x-axis shows the two levels of context, y-axis shows mean change in player distance. Negative values on the y-axis indicate that players move toward other players in every turn. Colour represents the two levels of environmental richness (b) behavioural effect of other player knowledge on change in player distance. People moved closer to others when the other player had good knowledge of the environment.

A linear mixed model showed a main effect of context on change in player distance (df=2.370e2, t=-5.417, p=1.49e-07; see Figure 6.2a). People preferred to stay closer to the other player when in a competitive context than in a neutral context. There was also interaction between environmental context and richness (df=6.616e4, t=-2.177, p=2.95e-2). Post-hoc tests revealed that environmental richness significantly predicted choices in neutral blocks (df= 3.31e4, t=2.083, p=3.72e-2) but not in competitive blocks.

Other player knowledge influences social learning choices

A linear mixed model showed an effect of other player knowledge on change in player distance (df=6.61e04, t=-3.199, p=1.38e-3; see Figure 6.2b). Participants tended to move closer to the other player when the other player's knowledge was good compared to poor.

Transdiagnostic factors explain wide range of mental health symptoms

A scree test showed a six-factor solution to explain variance across items in our battery of questionnaires. An exploratory factor analysis revealed factors that corresponded to the following dimensions: depression-anxiety, social thriving, pleasure, impulsivity, social assurance, and social deficit (see Figure 6.3). The first 4 factors—namely depression-anxiety, social thriving, pleasure, and impulsivity—were similar to those observed in the friend request study described in chapter 3.

Transdiagnostic factor corresponding to depression anxiety relates to change in player distance

There was a significant correlation between the trans-diagnostic factor of depression-anxiety and mean change in player distance (df = 186, r=0.17, t=2.314, p=2.17e-2; see Figure 6.3). The greater the change in player distance, indicating movement away from the other player, the greater was the participant depression-anxiety score.

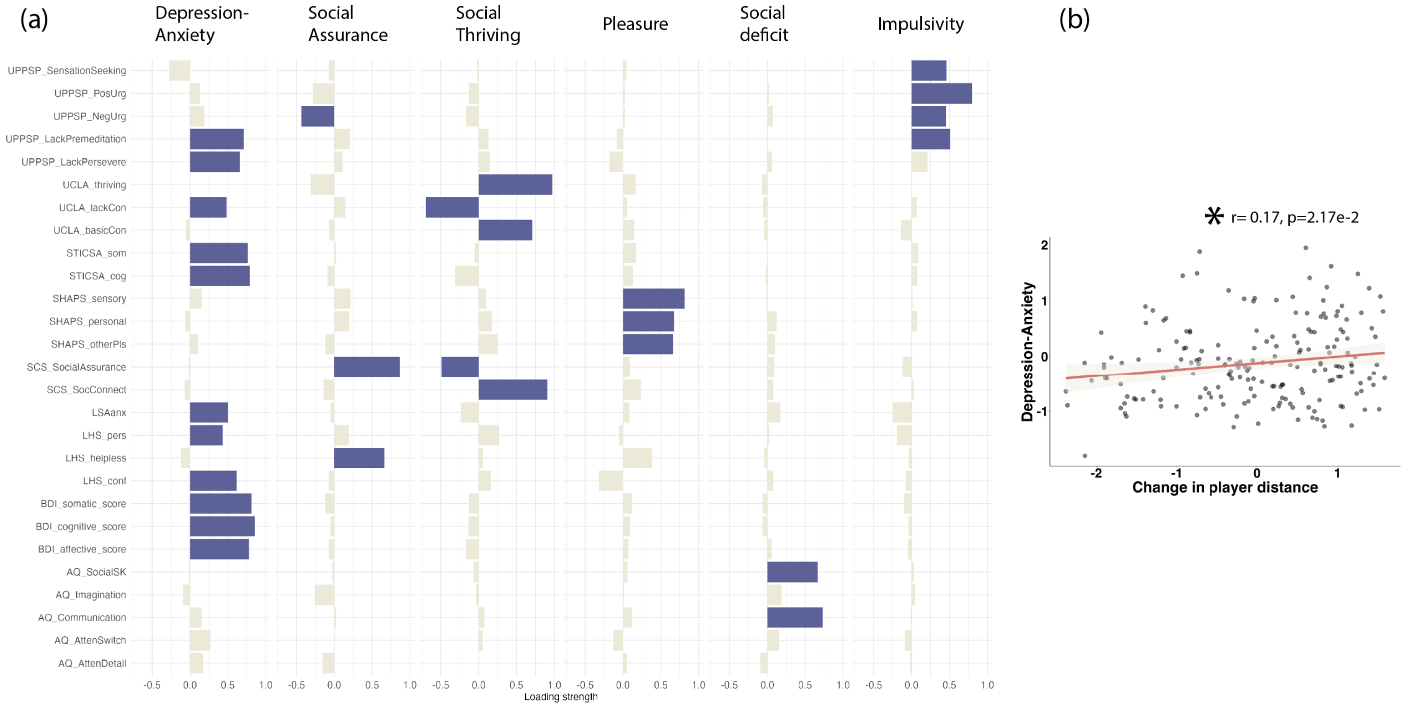

Figure 6.3: Factor structure and task-factor relationship. (a) factor structure obtained from psychiatric items presented before and after the present foraging task (b) relationship between change in player distance and the depression-anxiety factor. People who are score higher on depression-anxiety are likely to maintain more distance from the player on average.

6.4 Discussion

We devised a novel social decision-making task in order to better understand how humans balance pursuing rewards independently with learning from other people's knowledge. In this task, participants could gather reward independently or choose to stay closer to another player, either to exploit the other player's knowledge, or simply to benefit from the social connection and avoid risking isolation. The results suggest that people preferred staying closer to the other player irrespective of the environment they happened to be in, suggesting a pervasive tendency to maintain social company. This is consistent with the idea that humans may have a fundamental need to belong (Baumeister and Leary, 1995), mentioned ad nauseam across various chapters in this thesis, and a drive to affiliate that is similar to that observed in other social species like macaque monkeys (Deaner et al., 2005; Deaner and Platt, 2003).

The tendency to stay closer to others, however, was further amplified when the other player had good knowledge of their environment. This might suggest that while people prefer social company in general, they may be especially driven to seek proximity when there is an instrumental benefit like the opportunity to exploit others' knowledge. In addition, others' knowledge can be considered a proxy for social status, and the drive to exploit this knowledge can be considered analogous to the inclination that monkeys have to look longer at conspecifics with higher social status (Shepherd et al., 2006).

While context (competitive/neutral) significantly explained variance related to changes in player distance, the direction of this effect was contrary to that of our hypothesis. We expected people to stay closer to others in non-competitive contexts, but it is the competitive contexts in which people preferred proximity. This counter-intuitive behaviour might have occured because people would be risk-averse to independently explore in competitive blocks, as accumulating fewer points than their opponent would mean collecting no points at all. On the other hand, the absence of any constraints on total scores in neutral blocks might have encouraged more risky and exploratory behaviour, thereby permitting participants to stay further away from other players. We also found that participants stayed further away from others in rich blocks of neutral contexts but not of competitive contexts, further suggesting that the no-constraints nature of neutral contexts might have encouraged risk-taking.

Our hypothesis that participants would stay closer to others in non-competitive environments came from the Wittmann et al. (2016) study, where the researchers showed a "self-other mergence" effect in cooperative environments. In their study, co-operative environments were designed such that the total points gathered by the two players were cumulative. In our study, there was a competition and a neutral condition, but not a cooperation condition per se. This absence of a co-operative condition, i.e. an environment in which the scores were cumulative, might explain the discrepancy in behaviour observed between the Wittmann et al. (2016) study and the present study. In other words, non-competitive contexts may not be treated the same as co-operative contexts, and it is possible that if we introduced a condition of co-operation in the future, participants may choose to move closer to others compared to a competition condition.

Factor analyses of items from psychiatric questionnaires revealed similar factors to those observed in the friend request studies. At least 5 out of the 6 factors—namely social thriving, depression-anxiety, impulsivity, pleasure, and social assurance—were similar to those of the previous factor analyses from chapter four. The only new factor observed here was a social deficit factor, which arose largely as result of including scales measuring autism spectrum disorder. This "replication" of the factor structure suggests that solutions obtained through data driven methods can be robust and explain findings across multiple studies (Gillan et al., 2016).

We also observed that the depression-anxiety factor predicted change in player distance. In other words, participants that showed higher levels of anxiety-depression stayed further apart from the other player. However, interestingly, a factor like social thriving which measures social connection more directly did not predict proximity with other players. This might be because decisions to forage, while occurring in the proximity of others, are still a different kind of decision than inherently social decisions like sending friend requests. As a result, non-social psychiatric dimensions might be better suited to explain such decisions than social dimensions.

It is important to note that the results presented in this study are derived from an exploratory dataset. A confirmatory sample is needed to ascertain the validity and reproducibility of these results. A confirmatory dataset collection is planned in a few months.

Finally, future studies can shed light on the neural mechanisms underlying foraging decisions in the presence of others. Similar to the friend request studies described in chapters 3–5, we expect the DRN to be involved in tracking context in the present study (Priestley et al., 2024; Wittmann et al., 2020). We also expect regions that the DRN would project to, like the hypothalamus and aI, will be involved in tracking foraging contexts. Environmental richness in particular might be represented in the dopaminergic midbrain, following theoretical models of free operant behaviour that suggest animals track an average reward rate in dopaminergic regions like the substantia nigra and ventral tegmental area (Niv et al., 2007). Finally, other player knowledge, considered as a proxy for social status, might be represented in the interparietal sulcus in the parietal lobe, an area which is homologous to the lateral interparietal area in the macaque brain (Klein et al., 2008).

6.5 Conclusion

In this chapter, I described a novel social decision making task in which participants balanced foraging independently for rewards with staying close to others to learn from their knowledge. I showed that participants showed a general tendency to move closer to others. They also altered their decisions based on the context: they were more inclined to stay closer to others in competitive environments, and showed a preference for reward rich environments in neutral environments. Not surprisingly, they preferred to stay close to others when the other player's knowledge about the environment was good than when it was poor. Further, a factor analysis revealed a similar factor structure as that observed in the friend request studies, and the depression-anxiety factor in particular was related to the propensity to stay close to others. All findings described were derived from an exploratory dataset, and a confirmatory dataset is needed to corroborate these findings.

Acknowledgement: This study was part of an undergraduate thesis of Ingrid Yu, who designed the study, collected and analysed data with my guidance. I woud like to thank Ingrid for her role in undertaking this study.

Chapter 7

Discussion

In this thesis, I examined the influence of one's environment on their social decisions. In particular, in chapter two, I investigated how the friendliness and density of an environment would affect one's propensity to initiate social ties. Both friendliness and density significantly influenced participant friendship requesting behaviour. Friendlier and sparser blocks were associated with higher request rates, which were results analogous to those from animal foraging studies.

While in chapter two, I described the links between background environment and social affiliation choices, I did not investigate the mechanism underlying those choices. For instance, people might be sending a friend request owing to a fear of rejection, or in order to meet their Dunbar's number quota of friendships. Such behavioural mechanisms could be investigated by creating computational models with different friendship request strategies and assessing their fit to participants' true data.

In chapter three, I investigated the relationship between social affiliation choices and one's personality or psychiatric profile. To formulate a participant's psychiatric profile, I derived trans-diagnostic factors and discussed the advantages of using them over traditional diagnostic criteria. I then showed that such factors were linked to participant's behaviour in the friend request task. For instance, one's trans-diagnostic social thriving score was linked to the total amount of friendship requests submitted.

Trans-diagnostic factors carry the potential of decoupling the clinician and the diagnosis. As a result, these factors could be used to take mental health testing to the cloud. For instance, social media companies can use these factors to determine the effects of online social behaviour on mental health. Companies intending to administer digital therapies like Woebot can use these factors to assess the efficacy of their interventions.

In chapter four, I investigated the neural markers of social affiliation decisions. Environmental density was found to be represented in the network of predefined regions of interest spanning the DRN, Hb, hypothalamus, aI, area 9, SN, and VTA. Similarly, environmental friendliness interacted with action and showed activations in the same network of regions. Finally, DRN-aI and SN-aI connectivity likely covaried as a function of density and friendliness respectively.

These neural findings suggest that a dual system, one involving serotonergic neurons and the other involving dopaminergic neurons, might be involved in representing friendliness and density respectively. Further, the aI might be a “hub” that integrates contextual information and dispatches relevant details to the appropriate subcortical regions. These hypotheses could be tested using a causal manipulation of serotonergic and dopaminergic circuits using drugs like sertraline and risperidone respectively. Finally, the insula-as-a-hub hypothesis can be tested by sonicating the aI using TUS.

In chapter five, I described a novel method for predicting trans-diagnostic factor scores in studies that do not have the luxury of asking participants to complete an entire battery of questionnaires. This inability to acquire feature-rich data could either occur owing to monetary or time-related opportunity costs, or because a dataset has been already acquired. I further showed that model derived pleasure factor scores were related to SN-aI resting state connectivity in the HCP dataset.

Finally, in chapter six, I went beyond social affiliation decisions and described the role of the environment in influencing decisions of social learning. Participants’ completed a foraging task in which they chose between exploiting the knowledge of their co-player or independently exploring the environment. In general, participants preferred to stay close to their co-players, but this was especially the case in competitive environments, in reward-poor environments, and when the other player knowledge was good and worth exploiting. These findings suggested that the effect of the environment might be generally present across social decisions, and may not be limited to friendship or affiliation-based decisions.

While the studies mentioned reveal the importance of the role of the environment in social decisions, they are not without their limitations. For one, while the Friend Request Task aims to examine social affiliation decisions, it does not address whether the observed effects are domain-specific social effects. In other words, it does not determine whether background effects would hold if participants performed a similar non-social task involving, for instance, foraging-style approach-avoid decisions. For example, a future study could modify the design of the Friend Request Task to present abstract stimuli instead of faces, asking participants to select the stimuli they prefer. Behavioural and the corresponding neural results from such a task would help ascertain whether the background effects are specifically social in nature.

Another limitation of the current study design is the lack of insight into why participants varied their decisions in different social environments, and how this variation might link to their mental health profile. To better understand what shapes the relationship between mental health and social decisions, a Patient and Public Involvement (PPI) study could be conducted. PPI studies involve actively engaging patients and the public in the research process, using multimodal tools like qualitative interviews, surveys, and assessments. This approach can provide valuable insights into the lived experiences of participants and patients, and could further inform the development of targeted social interventions aimed at improving mental health outcomes.

An overarching limitation the findings described in chapters three and four is the lack of causal results. These findings, linking behaviour with mental health profile and neural bases, present correlational results, and do not establish causation. To understand the causal neural mechanisms, I have suggested various approaches, such as using drugs like Sertraline and Risperidone to test the involvement of serotonin and dopamine respectively, and interventions like ultrasound to examine the role of the insula as a key hub integrating social information. To test for any causal link between social affiliation decisions and participant mental health, social-specific interventions like asking participants to initiate conversation with strangers could be used (for example, similar to interventions used by Kardas et al. (2021)), and the effect of such interventions on participant mental health could be examined. On the other flipside, traditional mental health enhancing interventions like Cognitive Behavioural Therapy could be used to assess its effect on social behaviour. Such studies would provide a comprehensive understanding of the causal links between social behaviour and mental health and neural profiles outlined both in the Friend Request and Social Learning studies.

In the past decade, a significant proportion of our social interactions have moved online to social media platforms. In the Introduction, I reviewed the potential link between social media usage and mental health outcomes. Given the integration of social media into our social lives, it is important to study social media use and its impact on mental health. However, such investigations face several challenges, like the data on social media platforms being held by private companies who are often unwilling to invest in research or face negative publicity. Even if data is shared, it is not acquired in controlled settings and therefore any inferences would be confounded by several variables. A unique feature of the Friend Request Task is its resemblance to social media. This task offers a good balance between being naturalistic—resembling social media platforms—but is also controlled, as all stimulus and dependent variables are explicitly encoded and counterbalanced. Needless to say such a task is well suited for the MRI scanner as the timings of key events could be adjusted to suit features of the haemodynamic response function, making neural investigations possible. Future studies could use the features of the Friend Request Task to design experiments that resemble social media platforms, and therefore offer a novel way to test naturalistic internet-based social behaviour.

A major development in the last few years has been the advent of large language models (LLMs) such as OpenAI's GPT-4 and Anthropic Systems' Claude. Such models, trained on large datasets using deep learning techniques, possess the remarkable ability to simulate human-like conversations by predicting the next likely word based on a series of past words. Since a majority of our social interactions are verbal, a model's ability to simulate conversations opens up a new avenue for research in social behaviour. For instance, the Friend Request Task could be modified to not only present a face to send a friend request, but also offer an opportunity to engage in conversations with these faces. These AI-powered conversations could make the task feel more naturalistic, and also help acquire a rich dataset, highlighting the reasons why people choose to send friend requests. Further analyses, such as projecting language embeddings onto vector space or conducting sentiment analysis, could shed more light on the link between social decisions and participant psychiatric or personality profile.

In general, several studies could be undertaken in the future to both address the limitations of the studies described in chapters two through six, and to extend the foundations set by the Friend Request and Social Learning studies. These studies could range from drug intervention studies to test for the role of serotonin in representing background environments, all the way up to using LLMs to offer ecological validity and infer relationships between natural language responses and mental health profiles. By pursuing such diverse avenues, future studies could build a comprehensive understanding of the intricate link between social behaviour, neural mechanisms, and mental health, ultimately informing effective interventions and support systems.

All in all, given the importance of social connections in our lives, it is vital to understand how they start, and how they relate to our personalities and biologies. The vast majority of research conducted thus far had focused on features of individuals that led to social connection. In this thesis, I have suggested that beyond the individuals themselves, background and fundamental features of social environment can also influence who we connect with. Further, these background features are likely tracked by ancient neural circuitry, involving subcortical regions like the dorsal raphe nucleus and the substantia nigra. Moreover, individual variations in sensitivity to social environments may relate to individual variations in personality and psychiatric measures. Going forward, for us to form a complete picture of the science of social connection, my findings suggest that future work must take into account the role of the background environment in shaping social decisions.

Chapter 8

Conclusion

In this thesis, I investigated the behavioural, psychiatric, and neural bases of social decision making in different environments. In a friendship request task, people varied their behaviour in accordance with environmental background statistics. Such behaviour was found to be linked with trans-diagnostic psychiatric factors and with neural activations in pre-defined regions of interest. Finally, I showed that the influence of background environment extends beyond social affiliation decisions, and may be present in other social decisions like those that involve learning from others.

Bibliography

(2024). Adobe Illustrator. 67

Adolphs, R. (1994). Impaired recognition of emotion in facial expressions following bilateral damage to the human amygdala. *Nature*, 3(4):267a–274. 21

Adolphs, R., Gosselin, F., Buchanan, T., Tranel, D., Schyns, P., and Damasio, A. (2005). A mechanism for impaired fear recognition after amygdala damage. *Nature*, 433(7021):60–65. 21

Adolphs, R., Tranel, D., and Damasio, A. R. (1998). The human amygdala in social judgment. 393. 22

Allcott, H., Braghieri, L., Eichmeyer, S., and Gentzkow, M. (2020). The Welfare Effects of Social Media. *American Economic Review*, 110(3):629–676. 57

Allison, C., Auyeung, B., and Baron-Cohen, S. (2012). Toward brief "red flags" for autism screening: The short Autism Spectrum Quotient and the short Quantitative Checklist in 1,000 cases and 3,000 controls. *Journal of the American Academy of Child and Adolescent Psychiatry*, 51(2):202–212.e7. Publisher: Elsevier Inc. 80

Allman, J. M., Watson, K. K., Tetreault, N. A., and Hakeem, A. Y. (2005). Intuition and autism: a possible role for Von Economo neurons. *Trends in Cognitive Sciences*, 9(8):367–373. 43

Amat, J., Sparks, P. D., Matus-Amat, P., Griggs, J., Watkins, L. R., and Maier, S. F. (2001). The role of the habenular complex in the elevation of dorsal raphe nucleus serotonin and the changes in the behavioral responses produced by uncontrollable stress. *Brain Research*, 917(1):118–126. 37

Anderson, A. K. and Phelps, E. A. (2000). Expression without recognition: Contributions of the Human Amygdala to Emotional Communication. *Psychological Science*, 11(2):106–111. 21

Anderson, J., Jenkinson, M., and Smith, S. (2010). Non-linear registration, aka spatial normalisation. FMRIB technical report TR07JA2. *FMRIB technical report TR07JA2*. 93

Ang, Y. S., Lockwood, P., Apps, M. A., Muhammed, K., and Husain, M. (2017). Distinct subtypes of apathy revealed by the apathy motivation index. *PLoS ONE*, 12(1):1–15. ISBN: 1111111111. 79

APA (2024). Depression Assessment Instruments. 50

Apps, M. A. J., Rushworth, M. F. S., and Chang, S. W. C. (2016). The Anterior Cingulate Gyrus and Social Cognition: Tracking the Motivation of Others. *Neuron*, 90(4):692–707. Publisher: Elsevier. 26

Arnone, D., Wise, T., Fitzgerald, P. B., and Harmer, C. J. (2024). The involvement of serotonin in major depression: nescience in disguise? *Molecular Psychiatry*, 29(1):200–202. Publisher: Nature Publishing Group. 51

Bachevalier, J. (2000). The Amygdala, Social Cognition, and Autism. In Aggleton, J., editor, *The amygdala*. 22

Back, M. D., Schmukle, S. C., and Egloff, B. (2008). Becoming friends by chance. ISBN: 1467-9280(Electronic),0956-7976(Print) Issue: 5 Pages: 439–440 Place: Back, Mitja D.: Department of Psychology, University of Leipzig, Seeburgstrasse 14-20, Leipzig, Germany, 04103, mback@uni-leipzig.de Publication Title: Psychological Science Volume: 19. 11

Baker, K. G., Halliday, G. M., Hornung, J.-P., Geffen, L. B., Cotton, R. G. H., and To¨rk, I. (1991). Distribution, morphology and number of monoamine-synthesizing and substance P-containing neurons in the human dorsal raphe nucleus. *Neuroscience*, 42(3):757–775. Publisher: Elsevier. 33

Baron-Cohen, S., Baron-Cohen, S., Skinner, R., Skinner, R., Wheelwright, S. J., Wheelwright, S. J., Martin, J., Martin, J., Clubley, E., and Clubley, E. (2001). The Adult Autism Spectrum Quotient (AQ) Ages 16+. *Journal of Autism and Developmental Disorders*, 1(31):5–17. 46, 121

Bartholomew, K. and Horowitz, L. M. (1991). The Relationships Questionnaire (RQ). *Journal of personality and social psychology*, 61:226–244. 79

Basile, B. M., Schafroth, J. L., Karaskiewicz, C. L., Chang, S. W. C., and Murray, E. A. (2020). The anterior cingulate cortex is necessary for forming prosocial preferences from vicarious reinforcement in monkeys. *PLOS Biology*, 18(6):e3000677. Publisher: Public Library of Science. 25

Bauernfeind, A. L., de Sousa, A. A., Avasthi, T., Dobson, S. D., Raghanti, M. A., Lewandowski, A. H., Zilles, K., Semendeferi, K., Allman, J. M., Craig, A. D. B., Hof, P. R., and Sherwood, C. C. (2013). A volumetric comparison of the insular cortex and its subregions in primates. *Journal of Human Evolution*, 64(4):263–279. 41

Baumeister, R. F. and Leary, M. R. (1995). The Need to Belong: Desire for Interpersonal Attachments as a Fundamental Human Motivation. *Psychological Bulletin*, 117(3):497–529. 7, 8, 9, 117, 124

Bebbington, P., Hurry, J., Katz, R., Mcguffin, P., and Tennant, C. (1989). The risk of minor depression before age 65: Results from a community survey. *Psychological Medicine*, 19(2):393–400. 48

Beck, A. T. (1961). An Inventory for Measuring Depression. *Archives of General Psychiatry*, 4(6):561. 121

Beck, A. T., Steer, R. A., Ball, R., and Ranieri, W. F. (1996). Comparison of Beck Depression Inventories-IA and-II in Psychiatric Outpatients. *Journal of Personality Assessment*, 67(3):588–597. Publisher: Routledge. 80

Beck, A. T., Ward, C., Mendelson, M., Mock, J., and Erbaugh, J. (1960). Inventory for Measuring Depression. *Arch. Gen. Psychiatry*, pages 561–571. 46, 50

Beer, J. S., Heerey, E. A., Keltner, D., Scabini, D., and Knight, R. T. (2003). The Regulatory Function of Self-Conscious Emotion: Insights from Patients with Orbitofrontal Damage. *Journal of Personality and Social Psychology*, 85(4):594–604. 29

Behrens, T. E., Woolrich, M. W., Walton, M. E., and Rushworth, M. F. (2007). Learning the value of information in an uncertain world. *Nature Neuroscience*. ISBN: 1097-6256 (Print)\n1097-6256 (Linking) _eprint: NIHMS150003. 52

Beliveau, V., Svarer, C., Frokjaer, V. G., Knudsen, G. M., Greve, D. N., and Fisher, P. M. (2015). Functional connectivity of the dorsal and median raphe nuclei at rest. *NeuroImage*, 116:187–195. 33

Belujon, P. and Grace, A. A. (2017). Dopamine System Dysregulation in Major Depressive Disorders. *International Journal of Neuropsychopharmacology*, 20(12):1036–1046. 114

Berkman, L. F. and Syme, S. (1979). SOCIAL NETWORKS, HOST RESISTANCE, AND MORTALITY: A NINE-YEAR FOLLOW-UP STUDY OF ALAMEDA COUNTY RESIDENTS. *American Journal of Epidemiology*, 109(2):186–204. 6

Berridge, K. C. and Robinson, T. E. (1998). What is the role of dopamine in reward: hedonic impact, reward learning, or incentive salience? *Brain Research Reviews*, 28(3):309–369. 40

Berscheid, E. and Reis, H. (1998). Attraction and Close Relationships. 13

Bianciardi, M., Toschi, N., Edlow, B. L., Eichner, C., Setsompop, K., Polimeni, J. R., Brown, E. N., Kinney, H. C., Rosen, B. R., and Wald, L. L. (2015). Toward an In Vivo Neuroimaging Template of Human Brainstem Nuclei of the Ascending Arousal, Autonomic, and Motor Systems. *Brain Connectivity*, 5(10):597–607. 94

Blain, B. and Rutledge, R. B. (2020). Momentary subjective well-being depends on learning and not reward. *eLife*, 9:e57977. Publisher: eLife Sciences Publications, Ltd. 52

Bornstein, R. F. (1989). Exposure and Affect: Overview and Meta-Analysis of Research, 1968-1987. *Psychological Bulletin*, 106(2):265–289. 11

Bouras, N. N., Mack, N. R., and Gao, W.-J. (2023). Prefrontal modulation of anxiety through a lens of noradrenergic signaling. *Frontiers in Systems Neuroscience*, 17:1173326. 55

Bowlby, J. (1982). Attachment and loss: Retrospect and prospect. ISBN: 1939-0025(Electronic),0002-9432(Print) Issue: 4 Pages: 664–678 Place: Bowlby, John: Tavistock Clinic, 120 Belsize Lane, London, United Kingdom, NW 3 Publication Title: American Journal of Orthopsychiatry Volume: 52. 9

Bradburn, N. M. (1969). *The structure of psychological well-being.* Aldine, Oxford, England. Publication Title: The structure of psychological well-being. 6

Brailovskaia, J., Swarlik, V. J., Grethe, G. A., Schillack, H., and Margraf, J. (2023). Experimental longitudinal evidence for causal role of social media use and physical activity in COVID-19 burden and mental health. *Journal of Public Health*, 31(11):1885–1898. 57

Breiter, H. C., Etcoff, N. L., Whalen, P. J., Kennedy, W. A., Rauch, S. L., Buckner, R. L., Strauss, M. M., Hyman, S. E., and Rosen, B. R. (1996). Response and habituation of the human amygdala during visual processing of facial expression. *Neuron*, 17(5):875–887. 21

Bromberg-Martin, E. S., Matsumoto, M., and Hikosaka, O. (2010). Dopamine in Motivational Control: Rewarding, Aversive, and Alerting. *Neuron*, 68(5):815–834. 40

Brooks, J. C. W., Beckmann, C. F., Miller, K. L., Wise, R. G., Porro, C. A., Tracey, I., and Jenkinson, M. (2008). Physiological noise modelling for spinal functional magnetic resonance imaging studies. *NeuroImage*, 39(2):680–692. 94

Buckley, T. C., Parker, J. D., and Heggie, J. (2001). A psychometric evaluation of the BDI-II in treatment-seeking substance abusers. *Journal of Substance Abuse Treatment*, 20(3):197–204. 80

Buss, D. M. (1995). Evolutionary Psychology: A New Paradigm for Psychological Science. *Psychological Inquiry*, 6(1):1–30. 14

Butler, A. C., Chapman, J. E., Forman, E. M., and Beck, A. T. (2006). The empirical status of cognitive-behavioral therapy: A review of meta-analyses. *Clinical Psychology Review*, 26(1):17–31. 51

Byrne, D., Baskett, G. D., and Hodges, L. (1971). Behavioral indicators of interpersonal attraction. ISBN: 1559-1816(Electronic),0021-9029(Print) Issue: 2 Pages: 137–149 Place: United Kingdom Publication Title: Journal of Applied Social Psychology Volume: 1. 12

Báez-Mendoza, R., Harris, C. J., and Schultz, W. (2013). Activity of striatal neurons reflects social action and own reward. *Proceedings of the National Academy of Sciences of the United States of America*, 110(41):16634–16639. 23, 24

Báez-Mendoza, R. and Schultz, W. (2013). The role of the striatum in social behavior. *Frontiers in Neuroscience*, 7(7 DEC):1–14. 24, 27

Báez-Mendoza, R., van Coeverden, C. R., and Schultz, W. (2016). A neuronal reward inequity signal in primate striatum. *Journal of Neurophysiology*, 115(1):68–79. 25

Cacioppo, J. and Cacioppo, S. (2014a). Social Relationships and Health: The Toxic Effects of Perceived Social Isolation. *Bone*, 23(1):1–7. ISBN: 6176321972 _eprint: NIHMS150003. 7, 75

Cacioppo, J. T. and Cacioppo, S. (2014b). Social Relationships and Health: The Toxic Effects of Perceived Social Isolation: Social Relationships and Health. *Social and Personality Psychology Compass*, 8(2):58–72. 106, 114

Calhoon, G. G. and Tye, K. M. (2015). Resolving the neural circuits of anxiety. *Nature Neuroscience*, 18(10):1394–1404. Publisher: Nature Publishing Group. 55

Campbell, S. and MacQueen, G. (2004). The role of the hippocampus in the pathophysiology of major depression. *Journal of Psychiatry and Neuroscience*, 29(6):417–426. Publisher: Journal of Psychiatry and Neuroscience Section: Review Paper. 51

Cannon, C. M. and Palmiter, R. D. (2003). Reward without dopamine. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 23(34):10827–10831. 34

Cascio, C. J., Moore, D., and McGlone, F. (2019). Social touch and human development. *Developmental Cognitive Neuroscience*, 35(September 2017):5–11. Publisher: Elsevier. 24

Chaiken, S. (1979). Communicator physical attractiveness and persuasion. *Journal of Personality and Social Psychology*, 37(8):1387–1397. Place: US Publisher: American Psychological Association. 13

Christoph, G. R., Leonzio, R. J., and Wilcox, K. S. (1986). Stimulation of the lateral habenula inhibits dopamine-containing neurons in the substantia nigra and ventral tegmental area of the rat. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 6(3):613–619. 37

Clifford, M. M. and Walster, E. (1973). Research note: The effect of physical attractiveness on teacher expectations. *Sociology of Education*, 46(2):248–258. Place: US Publisher: American Sociological Assn. 14

Cohen, S., Doyle, W. J., Skoner, D. P., Rabin, B. S., and Gwaltney, J. M. (1997). Social ties and susceptibility to the common cold. *Journal of the American Medical Association*, 277(24):1940–1944. 79

Collis, A. and Eggers, F. (2022). Effects of restricting social media usage on wellbeing and performance: A randomized control trial among students. *PLOS ONE*, 17(8):e0272416. Publisher: Public Library of Science. 58

Coppen, A. (1967). The Biochemistry of Affective Disorders. *The British Journal of Psychiatry*, 113(504):1237–1264. 50

Cowen, P. J. and Browning, M. (2015). What has serotonin to do with depression? *World Psychiatry*, 14(2):158–160. _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1002/wps.20229. 50

Craig, A. (2009). How do you feel — now? The anterior insula and human awareness. *Nature Reviews Neuroscience*, 10(1):59–70. Publisher: Nature Publishing Group. 41, 42, 43

Craig, A. D., Chen, K., Bandy, D., and Reiman, E. M. (2000). Thermosensory activation of insular cortex. *Nature Neuroscience*, 3(2):184–190. Publisher: Nature Publishing Group. 42

Crump, M. J. C., McDonnell, J. V., and Gureckis, T. M. (2013). Evaluating Amazon's Mechanical Turk as a Tool for Experimental Behavioral Research. *PLOS ONE*, 8(3):e57410. Publisher: Public Library of Science. 86

Cuijpers, P., Noma, H., Karyotaki, E., Vinkers, C. H., Cipriani, A., and Furukawa, T. A. (2020). A network meta-analysis of the effects of psychotherapies, pharmacotherapies and their combination in the treatment of adult depression. *World Psychiatry*, 19(1):92–107. _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1002/wps.20701. 51

Cunningham, S. J., Turk, D. J., Macdonald, L. M., and Macrae, C. N. (2008). Yours or mine? Ownership and memory. *Consciousness and Cognition: An International Journal*, 17(1):312–318. Place: Netherlands Publisher: Elsevier Science. 17

Cuthbert, B. N. and Insel, T. R. (2013). Toward the future of psychiatric diagnosis: The seven pillars of RDoC. *BMC Medicine*, 11(1). 46, 47

Cyders, M. A., Littlefield, A. K., Coffey, S., and Karyadi, K. A. (2014). Examination of a short English version of the UPPS-P Impulsive Behavior Scale. *Addictive behaviors*, 39(9):1372–1376. Edition: 2014/03/03. 80

Cyranowski, J. M., Zill, N., Bode, R., Butt, Z., Kelly, M. A. R., Pilkonis, P. A., Salsman, J. M., and Cella, D. (2013). Assessing social support, companionship, and distress: National Institute of Health (NIH) Toolbox Adult Social Relationship Scales. *Health Psychology*, 32(3):293–301. Place: US Publisher: American Psychological Association. 108

Dafny, N. and Qiao, J. T. (1990). Habenular neuron responses to noxious input are modified by dorsal raphe stimulation. *Neurological Research*, 12(2):117–121. 37

Davidson, J. R., Hughes, D., Blazer, D. G., and George, L. K. (1991). Post-traumatic stress disorder in the community: an epidemiological study. *Psychological Medicine*, 21(3):713–721. 54

Daw, N. D., O'Doherty, J. P., Dayan, P., Seymour, B., and Dolan, R. J. (2006). Cortical substrates for exploratory decisions in humans. *Nature*, 441(7095):876–879. Publisher: Nature Publishing Group. 117

de Leeuw, J. R. (2015). jsPsych: A JavaScript library for creating behavioral experiments in a Web browser. *Behavior Research Methods*, 47(1):1–12. 64

De Waal, F. B. M. (2008). The Thief in the Mirror. *PLoS Biology*, 6(8):e201. 43

Deaner, R. O., Khera, A. V., and Platt, M. L. (2005). Monkeys Pay Per View: Adaptive Valuation of Social Images by Rhesus Macaques. *Current Biology*, 15(6):543–548. 84, 117, 125

Deaner, R. O. and Platt, M. L. (2003). Reflexive Social Attention in Monkeys and Humans. *Current Biology*, 13(18):1609–1613. 117, 125

Di Chiara, G. (2002). Nucleus accumbens shell and core dopamine: differential role in behavior and addiction. *Behavioural Brain Research*, 137(1):75–114. 41

Diener, E. (1984). Subjective Well-Being. *Psychological Bulletin*, 95(3):542–575. 5

Dion, K., Berscheid, E., and Walster, E. (1972). What is beautiful is good. ISBN: 1939-1315(Electronic),0022-3514(Print) Issue: 3 Pages: 285–290 Place: US Publication Title: Journal of Personality and Social Psychology Volume: 24. 14

DiStefano, C., Zhu, M., and Mîndrilã, D. (2009). Understanding and Using Factor Scores: Considerations for the Applied Researcher. *Practical Assessment, Research, and Evaluation Practical Assessment, Research, and Evaluation*. Publisher: University of Massachusetts Amherst. 81

DiTommaso, E., Brannen, C., and Best, L. A. (2004). Measurement and validity characteristics of the short version of the social and emotional loneliness scale for adults. *Educational and Psychological Measurement*, 64(1):99–119. 121

Downs, A. C. and Lyons, P. M. (1991). Natural observations of the links between attractiveness and initial legal judgments. *Personality and Social Psychology Bulletin*, 17(5):541–547. Place: US Publisher: Sage Publications. 13

Dunbar, R. I. (1993). Coevolution of neocortical size, group size and language in humans. *Behavioral and Brain Sciences*, 16(4):681–694. Publisher: Oxford Union Society. 15, 16

Dunbar, R. I. (1998). The social brain hypothesis. *Evolutionary Anthropology*, 6(5):178–190. 15

Dunbar, R. I. M. (2018). The Anatomy of Friendship. *Trends in Cognitive Sciences*, 22(1):32–51. 60, 73

Easterlin, R. A. (2003). Explaining happiness. *Proceedings of the National Academy of Sciences of the United States of America*, 100(19):11176–11183. ISBN: 1633144100. 6

Eisenberger, N. I. (2012). The neural bases of social pain: Evidence for shared representations with physical pain. *Psychosomatic Medicine*, 74(2):126–135. 25

Eisenberger, N. I., Lieberman, M. D., and Williams, K. D. (2003). Does rejection hurt? An fMRI study of social exclusion. *Science*, 302(5643):290–292. 25

Elkin, I. (1989). National Institute of Mental Health Treatment of Depression Collaborative Research Program: General Effectiveness of Treatments. *Archives of General Psychiatry*, 46(11):971. 51

Engeln, R., Loach, R., Imundo, M. N., and Zola, A. (2020). Compared to Facebook, Instagram use causes more appearance comparison and lower body satisfaction in college women. *Body Image*, 34:38–45. 57

Erritzoe, D., Godlewska, B. R., Rizzo, G., Searle, G. E., Agnorelli, C., Lewis, Y., Ashok, A. H., Colasanti, A., Boura, I., Farrell, C., Parfitt, H., Howes, O., Passchier, J., Gunn, R. N., Politis, M., Nutt, D. J., Cowen, P. J., Knudsen, G. M., and Rabiner, E. A. (2023). Brain Serotonin Release Is Reduced in Patients With Depression: A [11C]Cimbi-36 Positron Emission Tomography Study With a d-Amphetamine Challenge. *Biological Psychiatry*, 93(12):1089–1098. Publisher: Elsevier. 51

Etkin, A. and Wager, T. D. (2007). Functional Neuroimaging of Anxiety: A Meta-Analysis of Emotional Processing in PTSD, Social Anxiety Disorder, and Specific Phobia. *The American Journal of Psychiatry*, 164(10):1476–1488. 55

Fan, Z., Chang, J., Liang, Y., Zhu, H., Zhang, C., Zheng, D., Wang, J., Xu, Y., Li, Q.-J., and Hu, H. (2023). Neural mechanism underlying depressive-like state associated with social status loss. *Cell*, 186(3):560–576.e17. 36, 37

Faul, F., Erdfelder, E., Lang, A.-G., and Buchner, A. (2007). G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods*, 39(2):175–191. 63

Feeney, J. A. (2002). Attachment, marital interaction, and relationship satisfaction: A diary study. *Personal Relationships*, 9(1):39–55. Place: Feeney, Judith A.: U Queensland, School of Psychology, Queensland, QLD, Australia, 4072, J.Feeney@psy.uq.edu.au Publisher: Blackwell Publishing. 10

Festinger, L., Schachter, S., and Back, K. (1950). *Social pressures in informal groups; a study of human factors in housing.* Harper, Oxford, England. Publication Title: Social pressures in informal groups; a study of human factors in housing. 10

Filley, C. M. (2020). Social Cognition and White Matter: Connectivity and Cooperation. *Cognitive and Behavioral Neurology*, 33(1):67–75. 106

Foa, E. B., Huppert, J. D., Leiberg, S., Langner, R., Kichic, R., Hajcak, G., and Salkovskis, P. M. (2002). The obsessive-compulsive inventory: Development and validation of a short version. *Psychological Assessment*, 14(4):485–496. 80

Fong, H., Zheng, J., and Kurrasch, D. (2023). The structural and functional complexity of the integrative hypothalamus. *Science*, 382(6669):388–394. Publisher: American Association for the Advancement of Science. 35

Fountoulakis, K. N. and Tsapakis, E. M. (2024). Neither serotonin disorder is at the core of depression nor dopamine at the core of schizophrenia; still these are biologically based mental disorders. *Molecular Psychiatry*, 29(1):198–199. Publisher: Nature Publishing Group. 50

Fried, E. I. and Nesse, R. M. (2015). Depression is not a consistent syndrome: An investigation of unique symptom patterns in the STAR*D study. *Journal of Affective Disorders*, 172:96–102. 49

Fu, C. H. Y., Williams, S. C. R., Cleare, A. J., Brammer, M. J., Walsh, N. D., Kim, J., Andrew, C. M., Pich, E. M., Williams, P. M., Reed, L. J., Mitterschiffthaler, M. T., Suckling, J., and Bullmore, E. T. (2004). Attenuation of the Neural Response to Sad Faces in Major Depressionby Antidepressant Treatment: A Prospective, Event-Related Functional Magnetic Resonance ImagingStudy. *Archives of General Psychiatry*, 61(9):877–889. 51

Fu, W., Le Maître, E., Fabre, V., Bernard, J.-F., David Xu, Z.-Q., and Hökfelt, T. (2010). Chemical neuroanatomy of the dorsal raphe nucleus and adjacent structures of the mouse brain. *The Journal of Comparative Neurology*, 518(17):3464–3494. 33

Fusar-Poli, P., Placentino, A., Carletti, F., Landi, P., Allen, P., Surguladze, S., Benedetti, F., Abbamonte, M., Gasparotti, R., Barale, F., Perez, J., McGuire, P., and Politi, P. (2009). Functional atlas of emotional faces processing: a voxel-based meta-analysis of 105 functional magnetic resonance imaging studies. *Journal of Psychiatry and Neuroscience*, 34(6):418–432. Publisher: Journal of Psychiatry and Neuroscience Section: Review Paper. 21

Gabay, A. S. and Apps, M. A. J. (2021). Foraging optimally in social neuroscience: computations and methodological considerations. *Social Cognitive and Affective Neuroscience*, 16(8):782–794. 29

Gabay, A. S., Pisauro, A., O'Nell, K. C., and Apps, M. A. J. (2024). Social environment-based opportunity costs dictate when people leave social interactions. *Communications Psychology*, 2(1):1–13. Publisher: Nature Publishing Group. 32

Garvey, M. J., Noyes, R., Woodman, C., and Laukes, C. (1995). Relationship of generalized anxiety symptoms to urinary 5-hydroxyindoleacetic acid and vanillylmandelic acid. *Psychiatry Research*, 57(1):1–5. 54

Gauthier, I. and Nuss, P. (2015). Anxiety disorders and GABA neurotransmission: a disturbance of modulation. *Neuropsychiatric Disease and Treatment*, page 165. 55

Gazzaniga, M., Ivry, R. B., and Magnum, R. M. (2019). Cognitive Neuroscience. 16, 17, 18, 20, 21, 28

Gillan, C. M., Kosinski, M., Whelan, R., Phelps, E. A., and Daw, N. D. (2016). Characterizing a psychiatric symptom dimension related to deficits in goaldirected control. *eLife*, 5(MARCH2016):1–24. 47, 76, 86, 87, 126

Gillan, C. M. and Seow, T. X. (2020). Carving Out New Transdiagnostic Dimensions for Research in Mental Health. *Biological Psychiatry: Cognitive Neuroscience and Neuroimaging*, 5(10):932–934. Publisher: Society of Biological Psychiatry. 47, 48, 76, 81, 85

Giraldeau, L.-A. and Dubois, F. (2008). Chapter 2 Social Foraging and the Study of Exploitative Behavior. In *Advances in the Study of Behavior*, volume 38, pages 59–104. Elsevier. 31

Godlewska, B. R., Browning, M., Norbury, R., Cowen, P. J., and Harmer, C. J. (2016). Early changes in emotional processing as a marker of clinical response to SSRI treatment in depression. *Translational Psychiatry*, 6(11):e957. 51

Goodwin, R. D., Faravelli, C., Rosi, S., Cosci, F., Truglia, E., de Graaf, R., and Wittchen, H. U. (2005). The epidemiology of panic disorder and agoraphobia in Europe. *European Neuropsychopharmacology: The Journal of the European College of Neuropsychopharmacology*, 15(4):435–443. 53

Goren, C. C., Sarty, M., and Wu, P. Y. (1975). Visual following and pattern discrimination of face-like stimuli by newborn infants. *Pediatrics*, 56(4):544–549. 8

Gosling, S. D., Rentfrow, P. J., and Swann, W. B. (2003). A very brief measure of the Big-Five personality domains. *Journal of Research in Personality*, 37(6):504–528. 108

Grabenhorst, F., Báez-Mendoza, R., Genest, W., Deco, G., and Schultz, W. (2019). Primate Amygdala Neurons Simulate Decision Processes of Social Partners. *Cell*, 177(4):986–998.e15. 23

Grace, A. A. (1991). Phasic versus tonic dopamine release and the modulation of dopamine system responsivity: A hypothesis for the etiology of schizophrenia. *Neuroscience*, 41(1):1–24. Publisher: Elsevier. 40

Greenberg, P. E., Sisitsky, T., Kessler, R. C., Finkelstein, S. N., Berndt, E. R., Davidson, J. R. T., and Fyer, A. J. (1999). The Economic Burden of Anxiety Disorders in the 1990s. *The Journal of Clinical Psychiatry*, 60(7):5363. Publisher: Physicians Postgraduate Press, Inc. 53

Gruber-Baldini, A. L., Schaie, K. W., and Willis, S. L. (1995). Similarity in married couples: A longitudinal study of mental abilities and rigidity-flexibility. ISBN: 1939-1315(Electronic),0022-3514(Print) Issue: 1 Pages: 191–203 Place: US Publication Title: Journal of Personality and Social Psychology Volume: 69. 13

Grös, D. F., Antony, M. M., Simms, L. J., and McCabe, R. E. (2007). Psychometric properties of the State-Trait Inventory for Cognitive and Somatic Anxiety (STICSA): Comparison to the State-Trait Anxiety Inventory (STAI). ISBN: 1939-134X(Electronic),1040-3590(Print) Issue: 4 Pages: 369–381 Place: Antony, Martin M.: Department of Psychology, Ryerson University, 350 Victoria Street, Toronto, ON, Canada, M5B 2K3, mantony@ryerson.ca Publication Title: Psychological Assessment Volume: 19. 80

Gusnard, D. A. and Raichle, M. E. (2001). Searching for a baseline: Functional imaging and the resting human brain. *Nature Reviews Neuroscience*, 2(10):685–694. 17

Haddock, S. A., Weiler, L. M., Trump, L. J., and Henry, K. L. (2017). The Efficacy of Internal Family Systems Therapy in the Treatment of Depression Among Female

College Students: A Pilot Study. *Journal of Marital and Family Therapy*, 43(1):131–144. _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1111/jmft.12184. 51

Haidt, J. (2024). *The Anxious Generation: How the Great Rewiring of Childhood Is Causing an Epidemic of Mental Illness*. Penguin. 56

Haidt, J., Rausch, Z., and Twenge, J. M. (2024). Social Media and Mental Health: A Collaborative Review (ongoing). 56, 58

Hall, I. E., Hall, I. E., and Hall, J. A. (2019). No Title. 58

Harbaugh, W., Mayr, U., and Burghart, D. (2007). Neural Responses to Taxation and Voluntary Giving Reveal Motives for Charitable Donations. 6(June):1622–1626. 24

Harker, L. and Keltner, D. (2001). Expressions of positive emotion in women's college yearbook pictures and their relationship to personality and life outcomes across adulthood. ISBN: 1939-1315(Electronic),0022-3514(Print) Issue: 1 Pages: 112–124 Place: US Publication Title: Journal of Personality and Social Psychology Volume: 80. 6

Hazan, C. and Shaver, P. (1987). Romantic love conceptualized as an attachment process. ISBN: 1939-1315(Electronic),0022-3514(Print) Issue: 3 Pages: 511–524 Place: US Publication Title: Journal of Personality and Social Psychology Volume: 52. 9

Hewstone, M. and Stroebe, W. (2021). *An Introduction to Social Psychology*. John Wiley & Sons. 60, 75

Hikosaka, O. (2010). The habenula: from stress evasion to value-based decision-making. *Nature Reviews Neuroscience*, 11(7):503–513. Publisher: Nature Publishing Group. 36, 38

Hnasko, T. S., Sotak, B. N., and Palmiter, R. D. (2005). Morphine reward in dopamine-deficient mice. *Nature*, 438(7069):854–857. 34

Hoopes, A., Mora, J. S., Dalca, A. V., Fischl, B., and Hoffmann, M. (2022). SynthStrip: skull-stripping for any brain image. *NeuroImage*, 260:119474. 93

Hunt, M. G., Marx, R., Lipson, C., and Young, J. (2018). No More FOMO: Limiting Social Media Decreases Loneliness and Depression. Archive Location: world Publisher: Guilford Publications Inc. 57

Huys, Q. J., Daw, N. D., and Dayan, P. (2015). Depression: A Decision-Theoretic Analysis. *Annual Review of Neuroscience*, 38(1):1–23. 52

Hyon, R., Chavez, R. S., Chwe, J. A. H., Wheatley, T., Kleinbaum, A. M., and Parkinson, C. (2022). White matter connectivity in brain networks supporting social and affective processing predicts real-world social network characteristics. *Communications Biology*, 5:1048. 106

Inaba, K., Mizuhiki, T., Setogawa, T., Toda, K., Richmond, B. J., and Shidara, M. (2013). Neurons in Monkey Dorsal Raphe Nucleus Code Beginning and Progress of Step-by-Step Schedule, Reward Expectation, and Amount of Reward Outcome in the Reward Schedule Task. *The Journal of Neuroscience*, 33(8):3477–3491. 33

Ishimura, K., Takeuchi, Y., Fujiwara, K., Tominaga, M., Yoshioka, H., and Sawada, T. (1988). Quantitative analysis of the distribution of serotonin-immunoreactive cell bodies in the mouse brain. *Neuroscience Letters*, 91(3):265–270. 33

Iversen, S. D. and Iversen, L. L. (2007). Dopamine: 50 years in perspective. *Trends in Neurosciences*, 30(5):188–193. 41

Izuma, K., Saito, D. N., and Sadato, N. (2008). Processing of Social and Monetary Rewards in the Human Striatum. *Neuron*, 58(2):284–294. 24

Jenkinson, M., Bannister, P., Brady, M., and Smith, S. (2002). Improved Optimization for the Robust and Accurate Linear Registration and Motion Correction of Brain Images. *NeuroImage*, 17(2):825–841. 93

Jenkinson, M., Beckmann, C. F., Behrens, T. E. J., Woolrich, M. W., and Smith, S. M. (2012). FSL. *NeuroImage*, 62(2):782–790. 93

Jensen, D. E. A., Ebmeier, K. P., Suri, S., Rushworth, M. F. S., and Klein-Flügge, M. C. (2024). Nuclei-specific hypothalamus networks predict a dimensional marker of stress in humans. *Nature Communications*, 15:2426. 35

Johnson, M. H., Dziurawiec, S., Ellis, H., and Morton, J. (1991). Newborns' preferential tracking of face-like stimuli and its subsequent decline. *Cognition*, 40(1-2):1–19. 8

Kafetsios, K. and Nezlek, J. B. (2002). Attachment styles in everyday social interaction. *European Journal of Social Psychology*, 32(5):719–735. Publisher: John Wiley & Sons, Ltd. 10

Kampe, K. K. W., Frith, C. D., Dolan, R. J., and Frith, U. (2001). Reward value of attractiveness and gaze. ISBN: 1476-4687(Electronic),0028-0836(Print) Issue: 6856 Pages: 589–590 Place: Kampe, Knut K. W.: Insititute of Cognitive Neuroscience, University College London, 17 Queen Square, London, United Kingdom, WC1N 3AR, k.kamp@ucl.ac.uk Publication Title: Nature Volume: 413. 14

Kardas, M., Kumar, A., and Epley, N. (2021). Overly Shallow?: Miscalibrated Expectation Create a Barrier to Deeper Conversation. *Journal of Personality and Social Psychology*. 131

Karremans, J. and Finkenauer, C. (2021). Attraction and Close Relationships. In Hewstone, M. and Stroebe, W., editors, *An Introduction to Social Psychology*. British Psychological Society, John Wiley and Sons, seventh edition. 9, 12, 13

Kawachi, I. and Berkman, L. F. (2001). Social ties and mental health. *Journal of Urban Health*, 78(3):458–467. 6

Kelley, A. W., Macrae, C. N., Wyland, C. L., Caglar, S., Inati, S., and Heatherton, T. F. (2002). Finding the self? An event-related fMRI study. *Journal of Cognitive Neuroscience*, 14(5):785–794. 16

Kelly, Y., Zilanawala, A., Booker, C., and Sacker, A. (2018). Social Media Use and Adolescent Mental Health: Findings From the UK Millennium Cohort Study. *eClinicalMedicine*, 6:59–68. Publisher: Elsevier. 56

Keramati, M. and Gutkin, B. (2014). Homeostatic reinforcement learning for integrating reward collection and physiological stability. *eLife*, 3:1–26. 102

Kessler, R. C., Berglund, P., Demler, O., Jin, R., Merikangas, K. R., and Walters, E. E. (2005). Lifetime Prevalence and Age-of-Onset Distributions of DSM-IV Disorders in the National Comorbidity Survey Replication. *Archives of General Psychiatry*, 62(6):593–602. 53

Khalighinejad, N., Priestley, L., Jbabdi, S., and Rushworth, M. F. (2020). Human decisions about when to act originate within a basal forebrain-nigral circuit. *Proceedings of the National Academy of Sciences of the United States of America*, 117(21):11799–11810. 102

Kiesow, H., Dunbar, R. I. M., Kable, J. W., Kalenscher, T., Vogeley, K., Schilbach, L., Marquand, A. F., Wiecki, T. V., and Bzdok, D. (2020). 10,000 social brains: Sex differentiation in human brain anatomy. *Science Advances*, 6(12):eaaz1170. 114

Kleemans, M., Daalmans, S., Carbaat, I., and Anschütz, D. (2018). Picture Perfect: The Direct Effect of Manipulated Instagram Photos on Body Image in Adolescent Girls. *Media Psychology*, 21(1):93–110. Publisher: Routledge _eprint: https://doi.org/10.1080/15213269.2016.1257392. 57

Klein, J. T., Deaner, R. O., and Platt, M. L. (2008). Neural Correlates of Social Target Value in Macaque Parietal Cortex. *Current Biology*, 18(6):419–424. Publisher: Elsevier. 127

Klein-Flügge, M. C., Bongioanni, A., and Rushworth, M. F. S. (2022a). Medial and orbital frontal cortex in decision-making and flexible behavior. *Neuron*, 110(17):2743–2770. 26

Klein-Flügge, M. C., Jensen, D. E. A., Takagi, Y., Priestley, L., Verhagen, L., Smith, S. M., and Rushworth, M. F. S. (2022b). Relationship between nuclei-specific amygdala connectivity and mental health dimensions in humans. *Nature Human Behaviour*, 6(12):1705–1722. 107, 109

Knutson, B., Rick, S., Wimmer, G. E., Prelec, D., and Loewenstein, G. (2007). Neural Predictors of Purchases. *Neuron*, 53(1):147–156. 43

Kolling, N., Behrens, T. E. J., Mars, R. B., and Rushworth, M. F. S. (2012). Neural Mechanisms of Foraging. *Science*, 336(6077):95–98. Publisher: American Association for the Advancement of Science. 117

Korn, C. W., Prehn, K., Park, S. Q., Walter, H., and Heekeren, H. R. (2012). Positively biased processing of self-relevant social feedback. *Journal of Neuroscience*, 32(47):16832–16844. 24, 25

Korszun, A., Moskvina, V., Craddock, N., Ferrero, F., Gill, M., Brewster, S., and McGuffin, P. (2004). Familiality of Symptom Dimensions in Depression—Correction. *Archives of General Psychiatry*, 61(7):693. 48, 49

Krebs, J. R., Erichsen, J. T., Webber, M. I., and Charnov, E. L. (1977). Optimal prey selection in the great tit (Parus major). *Animal Behaviour*, 25(PART 1):30–38. 30, 61, 71, 72

Lan, D. C. L. and Browning, M. (2022). What Can Reinforcement Learning Models of Dopamine and Serotonin Tell Us about the Action of Antidepressants? *Computational Psychiatry*, 6(1):166–188. 52

Lange, K., Kühn, S., and Filevich, E. (2015). "Just another tool for online studies" (JATOS): An easy solution for setup and management of web servers supporting online studies. *PLoS ONE*, 10(6):1–14. 64

Langlois, J. H., Ritter, J. M., Casey, R. J., and Sawin, D. B. (1995). Infant attractiveness predicts maternal behaviors and attitudes. *Developmental Psychology*, 31(3):464–472. Place: US Publisher: American Psychological Association. 14

Langlois, J. H. and Roggman, L. A. (1990). Attractive Faces Are Only Average. *Psychological Science*, pages 1–7. ISBN: 9781626239777. 12

Lanza, I. R., Short, D. K., Short, K. R., Raghavakaimal, S., Basu, R., Joyner, M. J., McConnell, J. P., and Nair, K. S. (2008). Endurance Exercise as a Countermeasure for Aging. *Diabetes*, 57(11):2933–2942. 106, 114

Laruelle, M., Abi-Dargham, A., van Dyck, C. H., Rosenblatt, W., Zea-Ponce, Y., Zoghbi, S. S., Baldwin, R. M., Charney, D. S., Hoffer, P. B., and Kung, H. F. (1995). SPECT imaging of striatal dopamine release after amphetamine challenge. *Journal of Nuclear Medicine: Official Publication, Society of Nuclear Medicine*, 36(7):1182–1190. 40

Lawson, R. P., Seymour, B., Loh, E., Lutti, A., Dolan, R. J., Dayan, P., Weiskopf, N., and Roiser, J. P. (2014). The habenula encodes negative motivational value associated with primary punishment in humans. *Proceedings of the National Academy of Sciences*, 111(32):11858–11863. Publisher: Proceedings of the National Academy of Sciences. 37

Leary, M. R. and Tangney, J. P. (2012). *Handbook of Self and Identity.* Guilford Press. 43

Lecourtier, L. and Kelly, P. H. (2007). A conductor hidden in the orchestra? Role of the habenular complex in monoamine transmission and cognition. *Neuroscience & Biobehavioral Reviews*, 31(5):658–672. 37

Lee, R. M. and Robbins, S. B. (1995). Measuring Belongingness: The Social Connectedness and the Social Assurance Scales. *Journal of Counseling Psychology*, 42(2):232–241. 79, 121

Li, L., Zhang, L.-Z., He, Z.-X., Ma, H., Zhang, Y.-T., Xun, Y.-F., Yuan, W., Hou, W.-J., Li, Y.-T., Lv, Z.-J., Jia, R., and Tai, F.-D. (2021). Dorsal raphe nucleus to anterior cingulate cortex 5-HTergic neural circuit modulates consolation and sociability. *eLife*, 10:e67638. 34

Li, Y., Zhong, W., Wang, D., Feng, Q., Liu, Z., Zhou, J., Jia, C., Hu, F., Zeng, J., Guo, Q., Fu, L., and Luo, M. (2016). Serotonin neurons in the dorsal raphe nucleus encode reward signals. *Nature Communications*, 7(1):10503. 33

Lieberman, M. D. (2013). *Social: Why Our Brains are Wired to Connect.* OUP Oxford. Google-Books-ID: 7ZOJAAAAQBAJ. 43

Lieblich, S. M., Castle, D. J., Pantelis, C., Hopwood, M., Young, A. H., and Everall, I. P. (2015). High heterogeneity and low reliability in the diagnosis of major depression will impair the development of new drugs. *BJPsych open*, 1(2):e5–e7. 50

Liebowitz, M. R. (1987). Social Phobia. 22:141–173. Publisher: Karger Publishers. 79, 121

Lindquist, M. A., Loh, J. M., Atlas, L. Y., and Wager, T. D. (2009). Modeling the Hemodynamic Response Function in fMRI: Efficiency, Bias and Mis-modeling. *Neuroimage*, 45(1 Suppl):S187–S198. 94

Lindström, B., Bellander, M., Schultner, D. T., Chang, A., Tobler, P. N., and Amodio, D. M. (2021). A computational reward learning account of social media engagement. *Nature Communications*, 12(1):1311. Publisher: Nature Publishing Group. 58

Liu, Z., Lin, R., and Luo, M. (2020). Reward Contributions to Serotonergic Functions. 33, 34

Lockwood, P. L. and Klein-Flügge, M. C. (2020). Computational modelling of social cognition and behaviour—a reinforcement learning primer. *Social Cognitive and Affective Neuroscience*, (March):1–11. 26

Lockwood, P. L., Wittmann, M. K., Apps, M. A., Klein-Flügge, M. C., Crockett, M. J., Humphreys, G. W., and Rushworth, M. F. (2018). Neural mechanisms for learning self and other ownership. *Nature communications*, 9(1):4747. Publisher: Springer US. 17

Lubben, J., Blozik, E., Gillmann, G., Iliffe, S., Von Kruse, W. R., Beck, J. C., and Stuck, A. E. (2006). Performance of an abbreviated version of the lubben social network scale among three European community-dwelling older adult populations. *Gerontologist*, 46(4):503–513. 79

Luo, M., Zhou, J., and Liu, Z. (2015). Reward processing by the dorsal raphe nucleus: 5-HT and beyond. *Learning and Memory*, 22(9):452–460. 39, 89, 102

Ma, D. S., Correll, J., and Wittenbrink, B. (2015). The Chicago face database: A free stimulus set of faces and norming data. *Behavior Research Methods*, 47(4):1122–1135. ISBN: 1342801405325. 65

Matsumoto, M. and Hikosaka, O. (2007). Lateral habenula as a source of negative reward signals in dopamine neurons. *Nature*, 447(7148):1111–1115. 37

McCarthy, P., Cottaar, M., Webster, M., Fitzgibbon, S., and Craig, M. (2024). fslpy. 93

Mei, L., Osakada, T., and Lin, D. (2023). Hypothalamic control of innate social behaviors. *Science*, 382(6669):399–404. Publisher: American Association for the Advancement of Science. 36

Menon, V., Gallardo, G., Pinsk, M. A., Nguyen, V.-D., Li, J.-R., Cai, W., and Wassermann, D. (2020). Microstructural organization of human insula is linked to its macrofunctional circuitry and predicts cognitive control. *eLife*, 9:e53470. Publisher: eLife Sciences Publications, Ltd. 41

Miller, K. L., Alfaro-Almagro, F., Bangerter, N. K., Thomas, D. L., Yacoub, E., Xu, J., Bartsch, A. J., Jbabdi, S., Sotiropoulos, S. N., Andersson, J. L. R., Griffanti, L., Douaud, G., Okell, T. W., Weale, P., Dragonu, I., Garratt, S., Hudson, S., Collins, R., Jenkinson, M., Matthews, P. M., and Smith, S. M. (2016). Multimodal population brain imaging in the UK Biobank prospective epidemiological study. *Nature Neuroscience*, 19(11):1523–1536. 114

Mirsky, A. F. (1960). Studies of the Effects of Brain Lesions on Social. *Annals of the New York Academy of Sciences*, 85(1):785–794. 22

Mitchell, J. P., Macrae, C. N., and Banaji, M. R. (2005). Forming impressions of people versus inanimate objects: Social-cognitive processing in the medial prefrontal cortex. *NeuroImage*, 26(1):251–257. 19

Miyazaki, K., Miyazaki, K. W., and Doya, K. (2011). Activation of Dorsal Raphe Serotonin Neurons Underlies Waiting for Delayed Rewards. *Journal of Neuroscience*, 31(2):469–479. Publisher: Society for Neuroscience Section: Articles. 34

Miyazaki, K. W., Miyazaki, K., and Doya, K. (2012). Activation of Dorsal Raphe Serotonin Neurons Is Necessary for Waiting for Delayed Rewards. *The Journal of Neuroscience*, 32(31):10451–10457. 34

Mobbs, D., Trimmer, P. C., Blumstein, D. T., and Dayan, P. (2018). Foraging for foundations in decision neuroscience: insights from ethology. *Nature Reviews Neuroscience*, 19(7):419–427. Publisher: Nature Publishing Group. 29

Mobbs, D., Yu, R., Meyer, M., Passamonti, L., Seymour, B., Calder, A. J., Schweizer, S., Frith, C. D., and Dalgleish, T. (2009). A key role for similarity in vicarious reward. *Science*, 324(5929):900. 24

Mochcovitch, M. D., da Rocha Freire, R. C., Garcia, R. F., and Nardi, A. E. (2014). A systematic review of fMRI studies in generalized anxiety disorder: Evaluating its neural and cognitive basis. *Journal of Affective Disorders*, 167:336–342. 54

Molesworth, T., Sheu, L. K., Cohen, S., Gianaros, P. J., and Verstynen, T. D. (2015). Social network diversity and white matter microstructural integrity in humans. *Social Cognitive and Affective Neuroscience*, 10(9):1169–1176. 106

Moncrieff, J., Cooper, R. E., Stockmann, T., Amendola, S., Hengartner, M. P., and Horowitz, M. A. (2022). The serotonin theory of depression: a systematic umbrella review of the evidence. *Molecular Psychiatry*, pages 1–14. Publisher: Nature Publishing Group. 50

Montoya, R. M., Horton, R. S., and Kirchner, J. (2008). Is actual similarity necessary for attraction? A meta-analysis of actual and perceived similarity. *Journal of Social and Personal Relationships*, 25(6):889–922. ISBN: 0265407508096. 13

Morales, M. and Margolis, E. B. (2017). Ventral tegmental area: cellular heterogeneity, connectivity and behaviour. *Nature Reviews Neuroscience*, 18(2):73–85. Publisher: Nature Publishing Group. 114

Moreland, R. L. and Beach, S. R. (1992). Exposure effects in the classroom: The development of affinity among students. *Journal of Experimental Social Psychology*, 28(3):255–276. Place: Netherlands Publisher: Elsevier Science. 11

Morris, J. S., Friston, K. J., Büchel, C., Frith, C. D., Young, A. W., Calder, A. J., and Dolan, R. J. (1998). A neuromodulatory role for the human amygdala in processing emotional facial expressions. *Brain*, 121(1):47–57. 21

Morris, J. S., Smith, K. A., Cowen, P. J., Friston, K. J., and Dolan, R. J. (1999). Covariation of activity in habenula and dorsal raphé nuclei following tryptophan depletion. *NeuroImage*, 10(2):163–172. 38

Murray, E. A. (2007). The amygdala, reward and emotion. *Trends in Cognitive Sciences*, 11(11):489–497. 22, 50

Murray, R., Kendler, K., McGuffin, P., Wessely, S., and Castle, D. (2008). *Essential Psychiatry*. Cambridge University Press. 45, 46, 48, 49, 53, 54, 55, 75

Murray, R. J., Schaer, M., and Debbané, M. (2012). Degrees of separation: A quantitative neuroimaging meta-analysis investigating self-specificity and shared neural activation between self- and other-reflection. *Neuroscience and Biobehavioral Reviews*, 36(3):1043–1059. Publisher: Elsevier Ltd. 17

Murray, S. L., Holmes, J. G., Bellavia, G., Griffin, D. W., and Dolderman, D. (2002). Kindred spirits? The benefits of egocentrism in close relationships. ISBN: 1939-1315(Electronic),0022-3514(Print) Issue: 4 Pages: 563–581 Place: Murray, Sandra L.: State U New York at Buffalo, Park Hall, Buffalo, NY, US, 14260-4110, smurray@acsu.buffalo.edu Publication Title: Journal of Personality and Social Psychology Volume: 82. 13

Nair, A., Niyogi, R. K., Shang, F., Tabrizi, S. J., Rees, G., and Rutledge, R. B. (2021). Opportunity cost determines free-operant action initiation latency and predicts apathy. *Psychological Medicine*, pages 1–10. 84

Namboodiri, V. M. K., Rodriguez-Romaguera, J., and Stuber, G. D. (2016). The habenula. *Current Biology*, 26(19):R873–R877. 36, 37

Namkung, H., Kim, S.-H., and Sawa, A. (2017). The Insula: An Underestimated Brain Area in Clinical Neuroscience, Psychiatry, and Neurology. *Trends in Neurosciences*, 40(4):200–207. 42

National Institute of Mental Health (2021). Research Domain Criteria Initiative. Publication Title: National Institute of Mental Health. 46

Nielsen, M. A. (2015). *Neural Networks and Deep Learning*. Publisher: Determination Press. 105

Nimchinsky, E. A., Gilissen, E., Allman, J. M., Perl, D. P., Erwin, J. M., and Hof, P. R. (1999). A neuronal morphologic type unique to humans and great apes. *Proceedings of the National Academy of Sciences*, 96(9):5268–5273. Publisher: Proceedings of the National Academy of Sciences. 43

Nishikawa, T., Fage, D., and Scatton, B. (1986). Evidence for, and nature of, the tonic inhibitory influence of habenulointerpeduncular pathways upon cerebral dopaminergic transmission in the rat. *Brain Research*, 373(1-2):324–336. 37

Niv, Y., Daw, N. D., Joel, D., and Dayan, P. (2007). Tonic dopamine: Opportunity costs and the control of response vigor. *Psychopharmacology*, 191(3):507–520. 31, 32, 61, 62, 72, 84, 88, 127

Noritake, A., Ninomiya, T., and Isoda, M. (2018). Social reward monitoring and valuation in the macaque brain. *Nature Neuroscience*, 21(10):1452–1462. Publisher: Springer US. 27

Noritake, A., Ninomiya, T., and Isoda, M. (2021). Subcortical encoding of agent-relevant associative signals for adaptive social behavior in the macaque. *Neuroscience and Biobehavioral Reviews*, 125:78–87. Publisher: Elsevier Ltd. 24, 28

Ogawa, S. K., Cohen, J. Y., Hwang, D., Uchida, N., and Watabe-Uchida, M. (2014). Organization of Monosynaptic Inputs to the Serotonin and Dopamine Neuromodulatory Systems. *Cell Reports*, 8(4):1105–1118. Publisher: Elsevier. 33

Orben, A. and Przybylski, A. K. (2019). The association between adolescent well-being and digital technology use. *Nature Human Behaviour*, 3(2):173–182. Publisher: Nature Publishing Group. 56

Paton, J. J., Belova, M. A., Morrison, S. E., and Salzman, C. D. (2006). The primate amygdala represents the positive and negative value of visual stimuli during learning. *Nature*, 439(7078):865–870. 22

Pauli, W. M., Nili, A. N., and Tyszka, J. M. (2018). A high-resolution probabilistic in vivo atlas of human subcortical brain nuclei. *Scientific Data*, 5(1):180063. Publisher: Nature Publishing Group. 94

Paulus, M. P., Feinstein, J. S., Castillo, G., Simmons, A. N., and Stein, M. B. (2005). Dose-Dependent Decrease of Activation in Bilateral Amygdala and Insula by Lorazepam During Emotion Processing. *Archives of General Psychiatry*, 62(3):282–288. 55

Penfield, W. and Faulk, M. E. (1955). THE INSULA: FURTHER OBSERVATIONS ON ITS FUNCTION. *Brain*, 78(4):445–470. 41

Pilkington, P. D., Reavley, N. J., and Jorm, A. F. (2013). The Australian public's beliefs about the causes of depression: Associated factors and changes over 16 years. *Journal of Affective Disorders*, 150(2):356–362. 50

Pollak Dorocic, I., Fürth, D., Xuan, Y., Johansson, Y., Pozzi, L., Silberberg, G., Carlén, M., and Meletis, K. (2014). A whole-brain atlas of inputs to serotonergic neurons of the dorsal and median raphe nuclei. *Neuron*, 83(3):663–678. 33

Premack, D. and Woodruff, G. (1978). Does the chimpanzee have a theory of mind? ISBN: 1469-1825(Electronic),0140-525X(Print) Issue: 4 Pages: 515–526 Place: United Kingdom Publication Title: Behavioral and Brain Sciences Volume: 1. 18

Preuschoff, K., Quartz, S. R., and Bossaerts, P. (2008). Human Insula Activation Reflects Risk Prediction Errors As Well As Risk. *The Journal of Neuroscience*, 28(11):2745–2752. 42

Priestley, L., Chiew, M., Shahdloo, M., Mahmoodi, A., Cheng, X., Cleveland, R., Rushworth, M., and Khalighinejad, N. (2024). DORSAL RAPHE NUCLEUS CONTROLS MOTIVATIONAL STATE TRANSITIONS IN MONKEYS. preprint, Neuroscience. 31, 88, 89, 101, 102, 126

Primack, B. A., Shensa, A., Sidani, J. E., Whaite, E. O., Lin, L. y., Rosen, D., Colditz, J. B., Radovic, A., and Miller, E. (2017). Social Media Use and Perceived Social Isolation Among Young Adults in the U.S. *American Journal of Preventive Medicine*, 53(1):1–8. Publisher: Elsevier. 56

Proverbio, A. M. (2023). Sex differences in the social brain and in social cognition. *Journal of Neuroscience Research*, 101(5):730–738. _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1002/jnr.24787. 114

Pyke, G. H., Pulliam, H. R., and Charnov, E. L. (1977). Optimal Foraging: A Selective Review of Theory and Tests. *The Quarterly Review of Biology*, 52(2):137–154. 30, 60, 61, 71, 73

Quinless, F. and Nelson, M. (1988). Development of a measure of Learned Helplessness. *Nursing Research*, 37. 80, 121

R Core Team (2024). R: a language and environment for statistical computing. manual, R Foundation for Statistical Computing, Vienna, Austria. 67, 93, 110

Raichle, M. E., MacLeod, A. M., Snyder, A. Z., Powers, W. J., Gusnard, D. A., and Shulman, G. L. (2001). A default mode of brain function. *Proceedings of the National Academy of Sciences of the United States of America*, 98(2):676–682. 17

Ramsey, S. R., Thompson, K. L., McKenzie, M., and Rosenbaum, A. (2016). Psychological research in the internet age: The quality of web-based data. *Computers in Human Behavior*, 58:354–360. 86

Redgrave, P., Rodriguez, M., Smith, Y., Rodriguez-Oroz, M. C., Lehericy, S., Bergman, H., Agid, Y., DeLong, M. R., and Obeso, J. A. (2010). Goal-directed and habitual control in the basal ganglia: implications for Parkinson's disease. *Nature Reviews Neuroscience*, 11(11):760–772. Publisher: Nature Publishing Group. 39

Ree, M. J., French, D., MacLeod, C., and Locke, V. (2008). State–Trait Inventory for Cognitive and Somatic Anxiety. 121

Ritchie, S. J., Cox, S. R., Shen, X., Lombardo, M. V., Reus, L. M., Alloza, C., Harris, M. A., Alderson, H. L., Hunter, S., Neilson, E., Liewald, D. C. M., Auyeung, B., Whalley, H. C., Lawrie, S. M., Gale, C. R., Bastin, M. E., McIntosh, A. M., and Deary, I. J. (2018). Sex Differences in the Adult Human Brain: Evidence from 5216 UK Biobank Participants. *Cerebral Cortex (New York, N.Y.: 1991)*, 28(8):2959–2975. 114

Rogers, T. B., Kuiper, N. A., and Kirker, W. S. (1977). Self-reference and the encoding of personal information. ISBN: 1939-1315(Electronic),0022-3514(Print) Issue: 9 Pages: 677–688 Place: US Publication Title: Journal of Personality and Social Psychology Volume: 35. 16

Rogers-Carter, M. M., Varela, J. A., Gribbons, K. B., Pierce, A. F., McGoey, M. T., Ritchey, M., and Christianson, J. P. (2018). Insular cortex mediates approach and avoidance responses to social affective stimuli. *Nature Neuroscience*, 21(3):404–414. 114

Rohrbaugh, M. J., Shoham, V., and Coyne, J. C. (2006). Effect of Marital Quality on Eight-Year Survival of Patients With Heart Failure. *American Journal of Cardiology*, 98(8):1069–1072. 6

Roiser, J. P., Levy, J., Fromm, S. J., Nugent, A. C., Talagala, S. L., Hasler, G., Henn, F. A., Sahakian, B. J., and Drevets, W. C. (2009). The effects of tryptophan depletion on neural responses to emotional words in remitted depression. *Biological psychiatry*, 66(5):441–450. 38

Rosenberg, M. (1965). Society and the adolescent self-image. *Society and the Adolescent Self-Image*, pages 1–326. ISBN: 9781400876136. 80

RStudio Team (2020). RStudio: Integrated development environment for R. manual, RStudio, PBC., Boston, MA. 67, 93

Russel, D. (1996). UCLA Loneliness Scale (Version 3): Reliability, Validity, and Factor Structure. *Journal of Personality Assessment*, 36(6):ebi. 79, 121

Sanders, S. K. and Shekhar, A. (1995). Regulation of anxiety by GABAA receptors in the rat amygdala. *Pharmacology Biochemistry and Behavior*, 52(4):701–706. 55

Saper, C. B. and Lowell, B. B. (2014). The hypothalamus. *Current Biology*, 24(23):R1111–R1116. 35

Sartorius, A., Kiening, K. L., Kirsch, P., von Gall, C. C., Haberkorn, U., Unterberg, A. W., Henn, F. A., and Meyer-Lindenberg, A. (2010). Remission of Major Depression Under Deep Brain Stimulation of the Lateral Habenula in a Therapy-Refractory Patient. *Biological Psychiatry*, 67(2):e9–e11. 38

Sawaguchi, T. and Kudo, H. (1990). Neocortical development and social structure in primates. *Primates*, 31(2):283–289. 15

Saxe, R. and Baron-Cohen, S. (2006). Editorial: The neuroscience of theory of mind. *Social Neuroscience*, 1(3-4):1–9. ISBN: 1747-0927. 19

Saxe, R. R., Whitfield-Gabrieli, S., Scholz, J., and Pelphrey, K. A. (2009). Brain regions for perceiving and reasoning about other people in school-aged children. *Child Development*, 80(4):1197–1209. 19

Scholl, J. and Klein-Flügge, M. (2018). Understanding psychiatric disorder by capturing ecologically relevant features of learning and decision-making. *Behavioural Brain Research*, 355:56–75. 52

Scholl, J., Trier, H. A., Rushworth, M. F. S., and Kolling, N. (2022). The effect of apathy and compulsivity on planning and stopping in sequential decision-making. *PLOS Biology*, 20(3):e3001566. Publisher: Public Library of Science. 76

Schultz, W. (1998). Predictive reward signal of dopamine neurons. *Journal of Neurophysiology*, 80(1):1–27. 40

Schultz, W. (2007). Multiple Dopamine Functions at Different Time Courses. *Annual Review of Neuroscience*, 30(1):259–288. 40

Schultz, W., Dayan, P., and Montague, P. R. (1997). A neural substrate of prediction and reward. *Science*, 275(5306):1593–1599. 23

Schülke, O., Bhagavatula, J., Vigilant, L., and Ostner, J. (2010). Social bonds enhance reproductive success in male macaques. *Current Biology*, 20(24):2207–2210. 26

Seeley, W. W., Carlin, D. A., Allman, J. M., Macedo, M. N., Bush, C., Miller, B. L., and DeArmond, S. J. (2006). Early frontotemporal dementia targets neurons unique to apes and humans. *Annals of Neurology*, 60(6):660–667. _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1002/ana.21055. 43

Seo, H., Cai, X., Donahue, C. H., and Lee, D. (2014). Neural correlates of strategic reasoning during competitive games. *Science*, 346(6207):340–343. Publisher: American Association for the Advancement of Science. 44

Seymour, B., O'Doherty, J. P., Dayan, P., Koltzenburg, M., Jones, A. K., Dolan, R. J., Friston, K. J., and Frackowiak, R. S. (2004). Temporal difference models describe higher-order learning in humans. *Nature*, 429(6992):664–667. Publisher: Nature Publishing Group. 42

Shepherd, S. V., Deaner, R. O., and Platt, M. L. (2006). Social status gates social attention in monkeys. *Current Biology*, 16(4):R119–R120. Publisher: Elsevier. 125

Sherif, M., Harvey, O. J., White, B. J., Hood, W. R., Carolyn, W., and Green, C. D. (1961). Intergroup Conflict and Cooperation: The Robbers Cave Experiment. (Stage 3). 8

Singer, T., Seymour, B., O'Doherty, J., Kaube, H., Dolan, R. J., and Frith, C. D. (2004). Empathy for Pain Involves the Affective but not Sensory Components of Pain. *Science*, 303(5661):1157–1162. 20

Smith, A. L., Carvalho, A. F., and Solmi, M. (2024). Methodological concerns in umbrella review of serotonin and depression. *Molecular Psychiatry*, 29(1):203–204. Publisher: Nature Publishing Group. 50

Smith, S. M., Beckmann, C. F., Andersson, J., Auerbach, E. J., Bijsterbosch, J., Douaud, G., Duff, E., Feinberg, D. A., Griffanti, L., Harms, M. P., Kelly, M., Laumann, T., Miller, K. L., Moeller, S., Petersen, S., Power, J., Salimi-Khorshidi, G., Snyder, A. Z., Vu, A. T., Woolrich, M. W., Xu, J., Yacoub, E., Uğurbil, K., Van Essen, D. C., and Glasser, M. F. (2013). Resting-state fMRI in the Human Connectome Project. *NeuroImage*, 80:144–168. 109

Snaith, R. P., Hamilton, M., Morley, S., Humayan, A., Hargreaves, D., and Trigwell, P. (1995). A Scale for the Assessment of Hedonic Tone the Snaith–Hamilton Pleasure Scale. *British Journal of Psychiatry*, 167(1):99–103. Edition: 2018/01/02 Publisher: Cambridge University Press. 80, 121

Somerville, L. H., Wig, G. S., Whalen, P. J., and Kelley, W. M. (2006). Dissociable medial temporal lobe contributions to social memory. *Journal of Cognitive Neuroscience*, 18(8):1253–1265. 22

Spears, R. and Taushch, N. (2021). Prejudice and Intergroup Relations. In Hewstone, M. and Stroebe, W., editors, *An Introduction to Social Psychology*. John Wiley and Sons, Ltd. Section: 14. 8

Spunt, R. P., Meyer, M. L., and Lieberman, M. D. (2015). The Default Mode of Human Brain Function Primes the Intentional Stance. *Journal of Cognitive Neuroscience*, 27(6):1116–1124. 18

Stone, V. E., Baron-Cohen, S., and Knight, R. T. (1998). Frontal Lobe Contributions to Theory of Mind. *Journal of Cognitive Neuroscience*, 10(5):640–656. 28

Strasser, B. and Burtscher, M. (2018). Survival of the fittest: VO2max, a key predictor of longevity? *Frontiers in Bioscience-Landmark*, 23(8):1505–1516. Number: 8 Publisher: IMR Press. 106

Strauss, E. D., Curley, J. P., Shizuka, D., and Hobson, E. A. (2022). The centennial of the pecking order: current state and future prospects for the study of dominance hierarchies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 377(1845):20200432. Publisher: Royal Society. 117

Sui, J. and Humphreys, G. W. (2015). The Integrative Self: How Self-Reference Integrates Perception and Memory. *Trends in Cognitive Sciences*, 19(12):719–728. 17

Tajfel, H., Billig, M. G., Bundy, R. P., and Flament, C. (1971). Social categorization and intergroup behaviour. *European Journal of Social Psychology*, 1(2):149–178. 8

Teramoto, M. and Bungum, T. J. (2010). Mortality and longevity of elite athletes. *Journal of Science and Medicine in Sport*, 13(4):410–416. 106

Testard, C., Shergold, C., Acevedo-Ithier, A., Hart, J., Bernau, A., Negron-Del Valle, J. E., Phillips, D., Watowich, M. M., Sanguinetti-Scheck, J. I., Montague, M. J., Snyder-Mackler, N., Higham, J. P., Platt, M. L., and Brent, L. J. N. (2024). Ecological disturbance alters the adaptive benefits of social ties. *Science*, 384(6702):1330–1335. Publisher: American Association for the Advancement of Science. 7

Tomova, L., Wang, K. L., Thompson, T., Matthews, G. A., Takahashi, A., Tye, K. M., and Saxe, R. (2020). Acute social isolation evokes midbrain craving responses similar to hunger. *Nature Neuroscience*, 23(12):1597–1605. Publisher: Springer US. 84, 89, 117

Tranel, D. and Hyman, B. T. (1990). Neuropsychological correlates of bilateral amygdala damage. ISBN: 1538-3687(Electronic),0003-9942(Print) Issue: 3 Pages: 349–355 Place: US Publication Title: Archives of Neurology Volume: 47. 22

Trier, H., O'Reilly, J., Spiering, L., Ma, S., Kolling, N., Rushworth, M., and Scholl, J. (2023a). Emotions and individual differences shape foraging under threat. 31, 88, 101, 102

Trier, H. A., Khalighinejad, N., Hamilton, S., Harbison, C., Priestley, L., Laubach, M., Scholl, J., and Rushworth, M. F. (2023b). An ancient subcortical circuit decides when to orient to threat in humans. Pages: 2023.10.24.563636 Section: New Results. 89, 94

Twenge, J. M. and Campbell, W. K. (2019). Media Use Is Linked to Lower Psychological Well-Being: Evidence from Three Datasets. *Psychiatric Quarterly*, 90(2):311–331. 56

Twenge, J. M., Joiner, T. E., Rogers, M. L., and Martin, G. N. (2018). Increases in Depressive Symptoms, Suicide-Related Outcomes, and Suicide Rates Among U.S. Adolescents After 2010 and Links to Increased New Media Screen Time. *Clinical Psychological Science*, 6(1):3–17. Publisher: SAGE Publications Inc. 56

Ullsperger, M. and von Cramon, D. Y. (2003). Error monitoring using external feedback: specific roles of the habenular complex, the reward system, and the cingulate motor area revealed by functional magnetic resonance imaging. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 23(10):4308–4314. 37

Valjakka, A., Vartiainen, J., Tuomisto, L., Tuomisto, J. T., Olkkonen, H., and Airaksinen, M. M. (1998). The fasciculus retroflexus controls the integrity of REM sleep by supporting the generation of hippocampal theta rhythm and rapid eye movements in rats. *Brain Research Bulletin*, 47(2):171–184. 36

van de Waal, E., Borgeaud, C., and Whiten, A. (2013). Potent social learning and conformity shape a wild primate's foraging decisions. *Science (New York, N.Y.)*, 340(6131):483–485. 116

Van Essen, D. C., Smith, S. M., Barch, D. M., Behrens, T. E. J., Yacoub, E., and Ugurbil, K. (2013). The WU-Minn Human Connectome Project: An overview. *NeuroImage*, 80:62–79. 105, 109

Van Rossum, G. and Drake, F. L. (2009). *Python 3 Reference Manual*. CreateSpace, Scotts Valley, CA. 93

Vanheule, S., Desmet, M., Groenvynck, H., Rosseel, Y., and Fontaine, J. (2008). The factor structure of the beck depression inventory-II: An evaluation. *Assessment*, 15(2):177–187. 50

Vertes, R. P. (1991). A PHA-L analysis of ascending projections of the dorsal raphe nucleus in the rat. *The Journal of Comparative Neurology*, 313(4):643–668. 33

Vogel, T. A., Priestly, L., Cutler, J., Hogg, T., Khalighinejad, N., Garrett, N., Apps, M. A. J., Rushworth, M., and Lockwood, P. (2024). Humans decide to help others more often in poor environments. 32

Walum, H. and Young, L. J. (2018). The neural mechanisms and circuitry of the pair bond. *Nature Reviews Neuroscience*, 19(11):643–654. Publisher: Nature Publishing Group. 114

Ware, B. (2012). *The Top Five Regrets of the Dying: A Life Transformed by the Dearly Departing.* Hay House, Inc. Google-Books-ID: 4176DwAAQBAJ. 2

Weeden, J. and Sabini, J. (2005). Physical Attractiveness and Health in Western Societies: A Review. ISBN: 1939-1455(Electronic),0033-2909(Print) Issue: 5 Pages: 635–653 Place: Weeden, Jason: Department of Psychology, University of Pennsylvania, 3720 Walnut Street, Philadelphia, PA, US, 19104, jweeden@psych.upenn Publication Title: Psychological Bulletin Volume: 131. 14

Wicker, B., Keysers, C., Plailly, J., Royet, J. P., Gallese, V., and Rizzolatti, G. (2003). Both of us disgusted in My insula: The common neural basis of seeing and feeling disgust. *Neuron*, 40(3):655–664. 20

Williams, R. B., Barefoot, J. C., Califf, R. M., Haney, T. L., Saunders, W. B., Pryor, D. B., Hlatky, M. A., Siegler, I. C., and Mark, D. B. (1992). Prognostic Importance of Social and Economic Resources Among Medically Treated Patients With Angiographically Documented Coronary Artery Disease. *JAMA: The Journal of the American Medical Association*, 267(4):520–524. 6

Wise, R. A. (2004). Dopamine, learning and motivation. *Nature Reviews Neuroscience*, 5(6):483–494. Publisher: Nature Publishing Group. 39, 40

Wise, R. A. and Schwartz, H. V. (1981). Pimozide attenuates acquisition of lever-pressing for food in rats. *Pharmacology, Biochemistry, and Behavior*, 15(4):655–656. 39

Wise, T. and Dolan, R. J. (2020). Associations between aversive learning processes and transdiagnostic psychiatric symptoms in a general population sample. *Nature Communications*, 11(1):1–13. Publisher: Springer US. 76, 79

Wise, T., Marwood, L., Perkins, A. M., Herane-Vives, A., Joules, R., Lythgoe, D. J., Luh, W.-M., Williams, S. C. R., Young, A. H., Cleare, A. J., and Arnone, D. (2017). Instability of default mode network connectivity in major depression: a two-sample confirmation study. *Translational Psychiatry*, 7(4):e1105. 52

Wittmann, M. K., Fouragnan, E., Folloni, D., Klein-flügge, M. C., Chau, B. K. H., Khamassi, M., and Rushworth, M. F. S. (2020). Global reward state affects learning and activity in raphe nucleus and anterior insula in monkeys. *Nature Communications*, 11(2020):1–17. 31, 43, 88, 101, 126

Wittmann, M. K., Kolling, N., Akaishi, R., Chau, B. K. H., Brown, J. W., Nelissen, N., and Rushworth, M. F. S. (2016). Predictive decision making driven by multiple time-linked reward representations in the anterior cingulate cortex. *Nature Communications*, 7:12327. Publisher: The Author(s). 26, 44, 116, 125, 126

Wittmann, M. K., Lockwood, P. L., and Rushworth, M. F. (2018). Neural mechanisms of social cognition in primates. *Annual Review of Neuroscience*, 41(March):99–118. 44

Woolrich, M. W., Ripley, B. D., Brady, M., and Smith, S. M. (2001). Temporal Autocorrelation in Univariate Linear Modeling of FMRI Data. *NeuroImage*, 14(6):1370–1386. 94

Yoshida, K., Saito, N., Iriki, A., and Isoda, M. (2011). Representation of Others' Action by Neurons in Monkey Medial Frontal Cortex. *Current Biology*, 21(3):249–253. Publisher: Elsevier. 44

Zhang, C., Zhang, Y., Luo, H., Xu, X., Yuan, T.-f., Li, D., Cai, Y.-y., Gong, H., Peng, D.-h., Fang, Y.-r., Voon, V., and Sun, B. (2022). Bilateral Habenula deep brain stimulation for treatment-resistant depression: clinical findings and electrophysiological features. *Translational Psychiatry*, 12:52. 39