Social and Non-Social Reward Processing in Autism and Autistic Traits

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Abstract

Rewards are immensely important in human lives: They motivate us to engage in new behaviours and they reinforce previous ones. Reward responsiveness refers to the brain function that defines one's experiences of rewards and their motivational power. Its alterations have potentially stark consequences for development and functioning. In this vein, the social motivation theory suggests that the core socio-communicative impairments in autism spectrum conditions (ASC) may stem from deficient responsiveness to specifically social rewards in this population. However, the literature on this topic is inconclusive: Previous studies are methodologically heterogenous and offer mixed results. This dissertation includes four studies investigating responsiveness to social and non-social rewards with particular focus on ASC and autistic traits.

Study 1 aimed to investigate event-related brain potentials (ERPs) in anticipation and reception of smiles (social reward) and money (non-social reward) across autistic traits in the general population. In contrast to the social motivation theory, we found enhanced neuronal responses to both social and non-social rewards associated with higher levels of autistic traits.

Study 2 extended these findings to individuals diagnosed with ASC. In addition to ERPs, this study also included indexes of autonomic (pupil sizes) and behavioural (reaction times) reward processing. In line with the first experiment, autism and higher levels of autistic traits were linked to enhanced neuronal and autonomic processing, regardless of the reward type (smile or money). At the same time, the ASC group showed typical task performance and reported reduced behavioural reward responsiveness.

Study 3 investigated the effects of social familiarity and relevance on reward-related pupillary responses and explored their interplay with autistic traits. The results indicated a role of familiarity and rewarding context (i.e., whether positive feedback was contingent on behaviour). Smiling faces, especially of more familiar people, elicited stronger pupil responses when they were presented as a reward contingent on participants' performance, as compared to when they were passively viewed. These results emphasise that the reward value of a positive stimulus depends on action-outcome associations,

and, in the case of the social domain, on *who* is the source of the rewarding feedback.

Study 4 is a theoretical perspective that aimed to integrate and discuss insights from different lines of empirical work investigating reward responsiveness in the neurotypical population and in ASC. It introduces a multidimensionality view of rewards and discusses pitfalls and recommendations for empirical research contrasting neuronal responses to social and non-social rewards.

Across all studies, I provide evidence for multifaceted reward responsiveness in ASC and higher levels of autistic traits: atypical neuronal and autonomic processing, typical performance, and decreased self-reported reward sensitivity. These results are discussed in the light of the social motivation theory. Further, this dissertation identifies important aspects of reward processing in the general population, based on which I propose a definition of reward which differentiates it from a merely positive stimulus. Finally, I discuss this work in the broader framework of social neuropsychology research and identify the ways in which it can be further improved in future studies.

Keywords:

reward, reward responsiveness, autism, autistic traits, social motivation theory, neuropsychology, event-related potentials, pupillometry

Zusammenfassung

Belohnungen sind für unser Leben von enormer Bedeutung: Sie motivieren uns zu neuen und verstärken bereits gelernte Verhaltensweisen. Belohnungssensitivität bezeichnet jene Funktion des Gehirns, die Erfahrungen mit Belohnungen sowie daraus resultierender Motivationskraft assoziiert. Beeinträchtigungen dieser Funktion haben potenziell schwerwiegende Folgen für die Entwicklung und das Funktionsniveau eines Menschen. In diesem Sinne legt die Theorie der sozialen Motivation nahe, dass die zentralen sozio-kommunikativen Beeinträchtigungen, die für Autismus-Spektrum-Störungen (ASS) charakteristisch sind, auf eine mangelhafte Reaktionsfähigkeit auf spezifische soziale Belohnungen zurückzuführen sind. Die Literatur zu diesem Thema ist jedoch nicht eindeutig: Die bisherigen Studien sind methodisch uneinheitlich und liefern verschiedene Ergebnisse. Diese Dissertation umfasst vier Studien, die die Reaktionsfähigkeit auf soziale und nicht-soziale Belohnungen unter besonderer Berücksichtigung des Autismus und autistischer Merkmale untersuchen.

In Studie 1 wurden ereigniskorrelierte Hirnpotentiale (EKPs) bei der Erwartung und dem Erhalt von monetären und relevanten sozialen Belohnungen (ein Lächeln des Experimentators) unter Einbeziehung von autistischen Merkmalen in der Allgemeinbevölkerung untersucht. Im Gegensatz zur Theorie der sozialen Motivation fanden wir verstärkte neuronale Reaktionen, sowohl auf soziale als auch auf nicht-soziale Belohnungen, assoziiert mit erhöhten Ausprägungen autistischer Merkmale.

In Studie 2 wurden diese Ergebnisse auf Personen mit einer Autismus-Diagnose ausgedehnt und zusätzlich zu den EKPs auch Indizes der autonomen (Pupillengröße) und verhaltensbezogenen (Reaktionszeiten) Belohnungsverarbeitung einbezogen. In Übereinstimmung mit dem ersten Experiment waren Autismus und ein höheres Maß an autistischen Merkmalen mit einer verstärkten neuronalen und autonomen Verarbeitung verbunden, unabhängig von der Art der Belohnung (Lächeln des Experimentators und Geld). Gleichzeitig zeigte die ASS-Gruppe eine typische Aufgabenleistung und wies eine geringere Verhaltensreaktion auf Belohnungen auf.

Studie 3 untersuchte die Rolle von sozialer Vertrautheit und Relevanz auf belohnungsbezogene Pupillenreaktionen bei einer aktiven Aufgabe und beim passiven Betrachten. Die Ergebnisse weisen auf die Rolle der Vertrautheit und des Belohnungskontextes hin (d. h. darauf, ob positives Feedback vom Verhalten abhängig war). Lächelnde Gesichter, insbesondere von vertrauteren Personen, lösten nur während der aktiven Aufgabe, nicht aber während des passiven Betrachtens, verstärkte Pupillenreaktionen aus. Diese Ergebnisse unterstreichen, dass der Belohnungswert eines positiven Reizes einerseits von den Assoziationen zwischen Handlung und Ergebnis und andererseits, zumindest im sozialen Kontext, auch vom Ursprung des belohnenden Feedbacks abhängt.

Studie 4 ist eine theoretische Perspektive, die, basierend auf vorangegangenen empirischen Studien, Erkenntnisse über die Belohnungsempfindlichkeit in der neurotypischen Bevölkerung und im Autismus kombiniert und erweitert. Sie führt eine mehrdimensionale Sichtweise von Belohnungen ein und diskutiert Fallstricke und Empfehlungen für die empirische Forschung durch das Gegenüberstellen von neuronalen Reaktionen auf soziale und nicht-soziale Belohnungen.

In allen Studien konnte gezeigt werden, dass Autismus und höhere Ausprägungen an autistischen Merkmalen durch eine atypisch verstärkte neuronale und autonome Verarbeitung von Belohnungen gekennzeichnet sind – bei gleichzeitig typischer Leistung und geringerer selbstberichteter Sensitivität gegenüber Belohnungen. Diese Ergebnisse werden vor dem Hintergrund der Theorie der sozialen Motivation bei Autismus diskutiert. Darüber hinaus werden in dieser Dissertation wichtige Aspekte der Belohnungsverarbeitung in der Allgemeinbevölkerung hervorgehoben, auf deren Grundlage ich eine Definition einer Belohnung vorschlage, die sie von einem rein positiven Stimulus unterscheidet. Abschließend wird diese Arbeit im breiteren Rahmen der sozial-neuropsychologischen Forschung diskutiert und es werden Möglichkeiten vorgeschlagen, wie diese in zukünftigen Studien weiter verbessert werden kann.

Schlagwörter:

Belohnung, Belohnungsempfänglichkeit, Autismus, autistische Züge, Theorie der sozialen Motivation, Neuropsychologie, ereigniskorrelierte Potenziale, Pupillometrie

Contents

List of original publications

This dissertation is based on studies that have been published or are in preparation for submission in peer-reviewed journals.

Study 1:

Matyjek, M., Bayer, M., & Dziobek, I. (2020), Autistic Traits Affect Reward Anticipation but not Reception. *Scientific Reports 10*, 8396. doi: 10.1038/s41598-020-65345-x.

Study 2:

Matyjek, M., Bayer, M., & Dziobek, I. (pre-print, 2022), Reward Responsiveness Across Autism and Autistic Traits – Evidence from Neuronal, Autonomic, and Behavioural Levels. doi: 10.1101/2022.02.11.22270801.

Study 3:

Matyjek, M., Bayer, M., & Dziobek, I. (2021), Pupillary Responses to Faces are Modulated by Familiarity and Rewarding Context. *Brain Sciences 11*, 794. doi: 10.3390/brainsci11060794.

Study 4:

Matyjek, M., Meliss, S., Dziobek, I., & Murayama, K. (2020), A Multidimensional View on Social and Non-social Rewards. *Frontiers in Psychiatry, 11*, 818. doi: 10.3389/fpsyt.2020.00818.

1

Introduction

What is reward, what is autism, and how is reward processing atypical in this condition?

> *Learning is its own exceeding great reward.*
>
> William Hazlitt

1. Introduction

Rewards are crucial for life (Schultz, 2015). They are what makes us eat, play, and work. All organisms with brains move, explore, and approach objects which offer the greatest rewards, be it the best nutrients or mating partners. Receiving and consuming rewards is pleasurable and motivates future behaviours which could lead to more rewards. Identifying which behaviours are linked to desired outcomes (i.e., learning) is crucial for maximising the gains. This directly influences the probability of repeating or avoiding certain behaviours in the future. Put more formally, rewards are outcomes of one's motivated behaviour, which are desired and positive, and which are the base for learning and for reinforcing behaviour. In the human brain, pursuing and receiving rewards activate many structures, including the orbitofrontal cortex, anterior cingulate, insula, and subcortical areas such as ventral tegmentum, ventral pallidum, nucleus accumbens, caudate, hippocampus, and amygdala (Haber & Knutson, 2010).

Given its importance, disruptions of the reward function may result in significant cognitive, social, and behavioural impairments. Thus, studying the reward function is an important topic in human psychology. Indeed, reward atypicalities have been implicated in many psychopathologies, including autism (Aldridge-Waddon et al., 2020; Chevallier et al., 2012; Schwarz et al., 2020). However, although the last couple of decades witnessed a growing number of empirical studies investigating potential impairments in reward processing in autism – especially in the social domain, which is significantly impacted in this condition – the results are remarkably inconsistent. The aim of this dissertation is to contribute to and extend the understanding of social and non-social reward processing with particular focus on autism.

In the next chapters, I first elaborate on what constitutes a reward and its subparts in psychology, and how responsiveness to rewards can be

conceptualised. Further, I introduce autism, a condition characterised predominantly by social impairments, delineate how these impairments may be underlined by deficits in reward processing, and review empirical evidence for this claim. Building on those, I introduce four studies conducted as part of this dissertation, which aimed to investigate reward responsiveness with a particular focus on autism. In the last chapter, I summarise and interpret the results of the original work conducted in this project and discuss insights of this dissertation for the broader fields of autism, reward, and social neuropsychology research.

1.1 Reward responsiveness

1.1.1 Subjectivity of a reward's value

A reward's value is not its physical properties: no object (or event) is intrinsically rewarding (Schultz, 2015). What defines a reward is the potential to elicit approach behaviour, to induce pleasure (or lack of displeasure[1]), and to modulate behaviour. Naturally, some objects or events are more commonly rewarding than others. For example, food or sexual orgasm are sought after and enjoyed more universally than receiving good grades at school or experiencing beauty while watching paintings. Therefore, the subjectiveness of a reward's value is evident. This, together with the limited explanatory power of the physical characteristics of rewards, calls for the need to identify measurable neuronal and behavioural correlates of rewards within the receivers. For example, we can study a person's choices under different acquirable rewards. We can also monitor this person's brain activity and identify biomarkers of the reward functions (preference, pleasure, motivation, etc.). If a person chooses one object over another and in response to it shows larger activation in the brain structures linked to reward processing, we say that for this person, this object has higher reward value than the other one.

However, the same rewards can modulate behaviours of one individual differently than of another. Since the (subjective) reward value of objects and events is generated in the brain (and does not exist in the physical realm), its

[1] Considering reward processing (also in autism), research further investigates processing of neutral feedback (Neuhaus et al., 2015) and negative reinforcements (Damiano et al., 2015). However, this substantially broadens the research question investigated in this dissertation and hence, here I focus specifically on the responsiveness to positive rewarding outcomes.

neuronal activity is a marker of *reward responsiveness* of an individual. In that sense, reward responsiveness is a function of the brain, which defines the degree to which one experiences positive responses to rewards (with the potential to modulate behaviour). In an effort to describe this function empirically (i.e., at least to an extend detachedly from the subjective experience), researchers have identified components of reward responsiveness with distinct psychological and neuronal characteristics.

1.1.2 Reward phases: Anticipation and reception

Processing of a reward can be divided into at least two parts: the appetitive motivation towards the reward, called *reward anticipation*, and the pleasure from receiving the reward, called *reward reception* (Berridge, 1996; Berridge et al., 2009). They can be considered *phases* of reward processing, because typically they are temporally subsequent: Anticipation occurs when it is possible to obtain a certain reward and one needs to engage in a behaviour leading to it, and reception starts from the moment the reward is acquired.

These two phases are closely related to (and often interchangeably called) *'wanting'* and *'liking'* (Berridge, 1996, 1999). However, 'wanting' and 'liking' can also be viewed more broadly as core unconscious components of emotional states (Berridge, 1999). In that sense, the former corresponds to *incentive salience* attributed to objects or events, and the latter is the basic experience of *pleasure* or hedonic activation. Interestingly, the concepts of 'wanting' and 'liking' are not limited to emotions of positive valence. For example, one can be experiencing the positive desire ('wanting') of feeling fear while watching horror movies. Similarly, while awaiting feedback from another person, one may be anxious and excited at the same time.

1.1.2.1 Reward anticipation

Reward anticipation may be initiated either by a stimulus signalling availability of a reward, or by internal mental states directing attention towards a future reward and engaging in a behaviour leading to it. In the case of the latter, one needs to link a certain behaviour with the possible reward. For example, to *want* a mother's smile as a reward for a certain behaviour, a child must *know* (implicitly or explicitly) that the smile will follow this behaviour. Failure to make this connection hinders anticipation of the reward and its motivational power. This suggests that there are two components of 'wanting', a cognitive and a non-cognitive, possibly unconscious, desire (Berridge

& Robinson, 2016). For example, a recovering addict may cognitively and consciously want to avoid drugs, but still experience a non-cognitive desire to consume them.

Impairments in reward anticipation have been observed in numerous psychopathologies, to name a few, in attention-deficit/hyperactivity disorder (ADHD), schizophrenia, panic disorder, and addiction (Held-Poschardt et al., 2018; Leroy et al., 2020; Linnet, 2014; Schwarz et al., 2020). In some, the symptoms are linked to hypo- and in some to hyper-anticipation (Aldridge-Waddon et al., 2020). Thus, anticipation-related atypicalities are valuable transdiagnostic indexes of psychological conditions.

1.1.2.2 Reward reception

Receiving a reward is typically a positive experience. Studies have shown that higher magnitude of a reward elicits enhanced brain responses (e.g., Paul et al., 2020; Rosell-Negre et al., 2017). Any positive stimulus could potentially be a reward but does not have to. The same stimulus may have a different rewarding value when it is received in response to one's actions and when it is encountered without any contingency on one's behaviour. This difference between 'active' and 'passive' rewards has been shown to manifest on behavioural, neuronal, and psychophysiological levels. For example, 'active' money is rated as more rewarding and elicits larger electrodermal and striatal activation than 'passive' money (Bjork & Hommer, 2007; Zink et al., 2004).

1.1.2.3 Decoupling of the phases

As Berridge (Berridge, 1996, p. 1) noted, 'it seems axiomatic that we want the rewards we like, and like the rewards we want'. However, these two processes – reward 'wanting' and 'liking' – can become decoupled. A vivid manifestation of this is seen in addiction disorders: the 'wanting' is heightened, which corresponds to the characteristic craving of the target of addiction (Mitchell et al., 2018; Volkow et al., 2019), but the 'liking' is disproportionally smaller (Robinson & Berridge, 1993).

While many structures of the reward circuit are active in both anticipation and reception of a reward, the functional decoupling of those two is also supported by differences in neuronal activation (for an overview, see Figure 1-1). 'Wanting' is generated in the brain by extended neuronal systems mediated by dopamine. The key structure for this phase is the ventral striatum (VS). On the other hand, 'liking' is associated with smaller neuronal areas, which

include mainly the mid-anterior prefrontal cortex, and also parts of the nucleus accumbens (NAcc; Berridge & Robinson, 2016). In line with the spatial discrepancy between the two reward phases, pleasure-related areas of the NAcc constitute only 10% of its volume, whereas the remaining 90% are linked to 'wanting' (Berridge & Robinson, 2016). Thus, there is more potential for altered reward anticipation than for altered reward reception in the brain. This corresponds to more research indicating atypical reward anticipation than reception in psychological disorders.

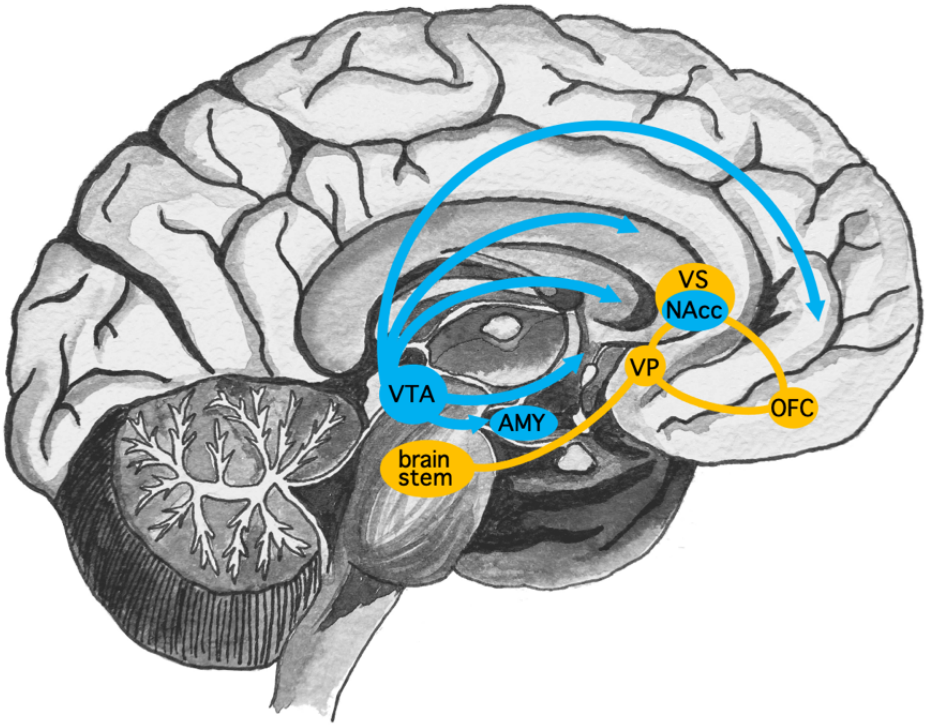

Figure 1-1 Schematic representation of the brain areas involved in 'wanting' (reward anticipation) and 'liking' (reward reception). Pathways and structures predominantly involved in 'wanting' and in 'liking' are marked in blue and yellow, respectively. Abbreviations: VTA = ventral tegmental area, AMY = amygdala, VS = ventral striatum, NAcc = nucleus accumbens, VP = ventral pallidum, OFC = orbitofrontal cortex. Handmade scientific illustration.

On the psychological level, while reward reception is relatively short, reward anticipation requires sustaining the motivation and attention resources over the period between the initialisation of 'wanting' and the delivery of the reward. The literature is inconsistent as to where anticipatory brain responses in studies are time-locked. Some studies operationalise anticipation as starting with a cue preceding a task leading to a reward (Kohls et al., 2011), some place it directly prior to reward reception (Stavropoulos & Carver, 2014a), and some

define it between reception of feedback (information on success or failure) and reception of a reward (Cox et al., 2015). Although few studies investigated multiple time points in anticipation during the same task, it is possible that anticipatory brain responses differ over time (Oumeziane et al., 2017). Therefore, while designing experiments, researchers should carefully consider where (or when) to time-lock reward anticipation.

1.1.3 Reward domains: Social and non-social

1.1.3.1 Common currency

The 'common currency' approach to reward, stemming from economics and decision neuroscience, proposes that all rewards are processed in the same brain structures and with the same mechanisms (Chib et al., 2009; Glimcher & Rustichini, 2004). Thus, social interactions evoke activation in the same structures as food, money, sex, and drugs (Richey et al., 2014). In this view, the brain's reward system is equipped to integrate numerous aspects of rewards, like magnitude, delay, salience, and subjective preferences, and to compute one unified value for all rewards. With this value, different rewards can be directly compared. Further, this evaluation encompasses subjective reward values, which has been shown to be reflected in the activation of the VS and the prefrontal cortex (Kable & Glimcher, 2007; Peters & Büchel, 2010).

1.1.3.2 Privileged standing of social signals

However, one category of rewards is often postulated to have an exceptional standing: social rewards. Social signals carry special importance for humans: We tend to automatically orient and attend to social stimuli, maintain and enhance relationships, and find (non-negative) social interactions rewarding (Chevallier et al., 2012). For example, attention is quickly captured by faces and bodies (Fletcher-Watson et al., 2008), prosocial behaviour like donating blood is not only inherently rewarding but even hindered by additional monetary compensation (Bowles, 2008), and humans exert effort to be seen more positively by others, e.g., as more likeable, competent, and attractive (Leary & Allen, 2011). In that vein, some studies propose that social rewards are processed in a distinctive way than their non-social counterparts, either in terms of separate brain structures, prioritised speed of processing, or selective impairments in certain conditions, e.g., in autism (Chevallier et al., 2012).

In those articles, authors predominantly assume a general intuitive understanding of which signals are social and which are not. For example, a smile or a verbal praise are social, whereas food or money are non-social. Although this distinction can become blurry, e.g., it may be argued that money is at least partially social as its very meaning is determined by a collective societal agreement (Galbin, 2014), the difference of social and non-social rewards is rarely operationalised in the reward literature (but see discussions on types of social rewards and incentives in psychology of emotion and personality, e.g., Buss, 1983). One reason for this is that social rewards are a wide-ranging set of verbal and non-verbal signals spanning over expressions (smile; Spreckelmeyer et al., 2009), communications (praise; Deci, 1971), behaviours (cooperation; Rilling et al., 2002), gestures (thumbs-up; Oumeziane et al., 2017), feelings (acceptance and good reputation; Izuma et al., 2008) and evaluations (social status; Zink et al., 2008). Nevertheless, although no clear definition is agreed upon in the field, there is an ongoing discourse about social rewards in contrast to non-social ones, which is based on a growing body of studies.

1.1.3.3 Combining social and non-social

While some studies find similar activation of the reward network for both social and non-social signals, others report distinctive neuronal processing (for a discussion, see Ruff & Fehr, 2014). A recent review of the neural correlates of reward anticipation provides evidence that the brain regions implicated in the processing of social and monetary incentives are indeed similar and include the ventral tegmental area (VTA), the VS, and the insula (Gu et al., 2019). Although the authors did not find any consistent involvement of previously reported brain regions involved specifically in the processing of social rewards (like the temporo-parietal junction; Barman et al., 2015; Carter et al., 2012; Spreckelmeyer et al., 2013), they observed some regions showing differences between the domains (albeit with similar functional connectivity profiles). Together, Gu and colleagues concluded that anticipation of social and monetary rewards engage similar brain regions but to different extents.

It is noteworthy that activation of the same structures does not imply involvement of the same mechanisms (Haxby et al., 2001) and hence overlapping brain structures activated by social and non-social rewards do not entail equal processing. For example, although the striatum is involved in processing of all rewards, it has been implicated as especially important for social information and behaviour as being capable of incorporating social actions and rewards (for a review, see Báez-Mendoza & Schultz, 2013). Thus, while both social and

non-social rewards may activate similar structures and mechanisms (and be therefore directly compared), they remain to an extend distinct categories.

1.1.4 Reward correlates: neuronal, autonomic, and behavioural

1.1.4.1 Neuronal bases

Functional magnetic resonance imaging (fMRI) studies help us understand which structures are involved in the processing of rewards and how they are connected. The reward circuit in the brain comprises multiple structures, including the VTA, the VS with the NAcc and the caudate, the amygdala, the insula, the prefrontal and orbitofrontal cortex (OFC), and the anterior cingulate cortex (Haber & Knutson, 2010). fMRI research shows that the VTA, the core node of the dopaminergic projections in the brain, and one of its main targets, the VS, are active during reward anticipation and in response to cues indicating future rewards (Haber & Knutson, 2010). Remarkably, the activation of the VS (specifically, the NAcc) is proportionally related to the magnitude of the rewards (Knutson et al., 2001). The insula, receiving input from the VTA, the VS, and the amygdala, is crucial in coding motivational salience of stimuli (Seeley et al., 2007). The amygdala assesses the saliency of stimuli, especially those which are emotionally laden, and projects to the VS and the OFC, which forms a representation of the value of a future reward.

1.1.4.2 Electroencephalography

To address how reward processing in the brain unfolds over time, a method allowing event-related measurements is needed. While fMRI has a high spatial resolution, its temporal resolution is vastly outperformed by electroencephalography (EEG), which can track brain activity with a millisecond precision. The EEG signals can be portioned into event-related potentials (ERPs). Several ERP components have been indicated as neuronal indexes of reward processing. Those of particular interest are the P3, the contingent negativity variation (CNV), and the stimulus-preceding negativity (SPN).

The P3 is a positive deflection peaking around 300ms after the onset of a stimulus at parietal areas. It is well-documented in the field of cognitive neuroscience for its involvement in allocating attentional resources (Kappenman & Luck, 2012). In the context of reward processing, it is sensitive to both reward magnitude and outcome valence, with larger amplitudes for more

rewarding and for positive outcomes (Wu & Zhou, 2009). Due to its role in evaluating reward salience, the P3 has been proposed to reflect the activity of the locus coeruleus-norepinephrine (LC-NE) system, which is strongly connected to the reward circuit (Nieuwenhuis et al., 2005).

The CNV and the SPN are both slow, negative waves over the central and parietal sites, which reflect anticipatory processes for future events (Novak & Foti, 2015). While both are elicited in response to a stimulus indicating an upcoming event, the CNV is observed prior to performing an action and the SPN prior to receiving important information, e.g., feedback (Brunia et al., 2012). Both have been previously associated with coding motivational value and saliency of stimuli during reward anticipation (Broyd et al., 2012; Brunia et al., 2012).

1.1.4.3 Autonomic indexes

Measures of the autonomic nervous system (ANS) offer complementary correlates of reward processing. The link between the ANS and reward processing is vivid in the involvement of the former in approach and avoidance (Neuhaus et al., 2015), which underlie motivated behaviours towards rewards and away from punishments. Moreover, stimulation of the VTA results in increases in blood pressure and heart rate, both controlled by the sympathetic branch of the ANS (van den Buuse, 1998). A particularly useful index of the ANS activity in reward research is the pupil size. The course of pupil dilation and constriction is a viable indirect measurement of the LC activity, which plays a major role in integrating motivationally relevant information (Aston-Jones et al., 1999; Bast et al., 2018; Bouret & Richmond, 2015). Accordingly, pupil sizes have been shown to vary with reward-related processes including attention allocation, effort, and anticipation of a reward (Carsten et al., 2021).

1.1.4.4 Behaviour

A number of behavioural measurements are targeted in reward research, e.g., reaction times (e.g., Kohls et al., 2009), accuracy (e.g., Garretson et al., 1990), effort (Dubey et al., 2015), approach behaviour (Kim et al., 2015), and choice (Watson et al., 2015). The targeted behavioural outcome depends largely on the task employed in each study. The cued incentive delay task is a well-established and well-documented behavioural task often used in reward research (Knutson et al., 2005). It involves the presentation of a cue which indicates possible outcomes in each trial, followed by a task

(e.g., a reaction time task to a simple target), and feedback. This paradigm owes its popularity in reward research to allowing separate measurements of reward anticipation and reception.

1.1.5 Conclusion: Reward responsiveness

Rewards are immensely important for human functioning. Since rewarding value is not an inherent property of any object or event, it is to a degree subjective and may differ between individuals. This subjective responsiveness to rewards can be measured. Research has identified several neuronal, autonomic, and behavioural indexes of reward responsiveness in its two phases: anticipation (when we 'want' a reward, work towards getting it, and prepare to acquire it) and reception (when we receive a reward and 'like' it). While different types of rewards are processed in similar brain structures, social rewards are to an extend distinct and privileged. One prominent argument for this dissociation comes from autism, which may be characterised by atypical responses to specifically social rewards. To elucidate this, in the next chapter I characterise autism with the focus on reward responsiveness in this population.

1.2 Autism

1.2.1 Characteristics of autism

The Diagnostic and Statistical Manual of Mental Disorders (DSM-5; American Psychiatric Association, 2013) describes autism spectrum disorders (abbreviated as ASD, however, I will use the term 'autism' or the abbreviation 'ASC' for 'autism spectrum *condition'*[2]) as a childhood-onset

[2] The term 'autism spectrum *condition'* (instead of *disorder*, the medical term) eases the heavily psychopathologic terminology and associations with illnesses or diseases, which are unwelcomed by many individuals with this diagnosis. This is in line with the idea of *neurodiversity*, which emphasises variability in the brain 'wiring' across people, promoting inclusiveness instead of labelling those with 'diseases' in contrast to those who are 'healthy'. Majority of the research on reward processing in autism is conducted with 'high-functioning' (see discussion on the dichotomous use of high vs. low functioning individuals in Fennell & Johnson, 2021) persons as participation in such studies requires sufficient language competency and the flexibility to perform in a new environment (laboratory), often under novel circumstances (e.g., with an EEG cap). This is also the case for all subjects diagnosed with autism in this dissertation, for which reason ASC is an appropriate term in this work. At the same time, it should be noted that the word *disorder*

neurodevelopmental disorder characterised by symptoms categorised into two groups: 1) social communication and interaction deficits, and 2) restricted, repetitive patterns of behaviour. The first group includes disordered language, problems with non-verbal communication, and deficits in socio-emotional reciprocity, like reduced sharing of emotions or failure to initiate social interactions. The second group includes stereotyped movements and use of objects or speech, isolated interests of excessive intensity, hyper- and hypo-sensitivity to sensory input, rigidity in thinking, and instances of sameness, inflexibility, and ritualisation.

Autism is a life-long condition with high prevalence of 0.6 – 1% (Simonoff & Chandler, 2008), and varying but increasing estimations around the world (Chakrabarti & Fombonne, 2005; Chiarotti & Venerosi, 2020). The social difficulties experienced by those with autism can be a great burden on themselves, their relatives, and the society. This makes ASC a major public health concern (Newschaffer & Curran, 2003). Despite years of research and considerable body of literature on the topic, the causes and underpinnings of autism remain unclear, and there is paucity of evidence-based effective behavioural or pharmacological treatment options (Masi et al., 2017). Regrettably, little understanding of this condition caused many harmful myths and misconceptions to grow over the years, starting from stigmatisation as a mental retardation, through the 'refrigerator mother' theory for children's severe emotional deficits, to the association between vaccination and autism (Davidson, 2017). Despite scientific evidence discrediting those misconceptions, many of them persist in the public's mind to this day.

Thus, continuous effort to increase the understanding of the mechanisms and the functioning in autism is needed to identify future treatment options and to increase wellbeing of those affected. A research line of particular importance is the identification of endophenotypes of autism based on reliable biomarkers (e.g., with neuroimaging and EEG), which could facilitate early detection of autism and potentially improve interventions through customisation to particular impairments (Neuhaus et al., 2010). However, this notable research endeavour is challenged by the complexity of ASC in terms of the

is a part of the medical term for autism, and it may be indeed more accurate especially for those with severe symptoms who are unable to function without substantial support.

intergroup diversity of severity, phenomenological manifestations, biological underpinnings, and substantial rates of comorbidities.

1.2.2 Heterogeneity of the spectrum

The word 'spectrum' emphasises that autism is heterogenous in terms of clinical symptomatology, aetiology, neurobiology, and severity (Bauman, 2010). Under the DSM-5, ASD is a unifying term for previously separate diagnoses, like autistic disorder, high functioning autism, Asperger's syndrome, pervasive developmental disorder not otherwise specified, etc (American Psychiatric Association, 2013). ASC spans over various difficulty types and severities, whose higher levels are associated with decreased independent functioning and increased need for support. Given the heterogeneity of ASC, it is not likely that a single aetiology could explain the broad symptomatology of this condition (Murdoch & State, 2013).

Moreover, ASC is often accompanied by numerous psychological and physical comorbidities (Bauman, 2010; Lai et al., 2019; Masi et al., 2017; Mazzone et al., 2012). For example, social anxiety disorder (SAD) shares phenotypic characteristics with ASC, like socio-communicative challenges (avoidance, withdrawal, and lack of prosocial behaviours) and around 20% of adults with autism are also diagnosed with SAD (Bejerot et al., 2014). Adding to the complexity, the convention for co-diagnoses changes with growing understanding of autism due to advances in clinical care and mounting research literature. For example, although up to 25% of youth with ADHD meet the criteria for ASC and even up to 70% of those with ASC have comorbid ADHD, until recently the diagnostic standards prohibited simultaneous diagnosis of both (Antshel et al., 2016). Despite diagnostic challenges, identification of the co-occurring conditions is crucial for providing appropriate health care and it has the potential to support more accurate genotypic identification of clinically informed subtypes of ASC (Bauman, 2010).

1.2.3 Autistic traits in the general population and in autism

There has been a growing attention towards recognising *autistic traits* in individuals not meeting the diagnosis criteria but displaying autism-like symptoms and behaviours. Autistic traits were first discussed in relation to close relatives of the patients. The term 'broad autism phenotype' was proposed to encompass milder expressions of the condition in non-autistic

individuals with diagnosed relatives (e.g., Hurley et al., 2007). These expressions are believed to indicate genetic liability for autism.

In the recent decades it has been recognised that the 'sub-threshold' autistic traits are not limited to the relatives of diagnosed individuals but are instead distributed normally in the general population (Allison et al., 2008; Baron-Cohen, Wheelwright, Skinner, et al., 2001; Hoekstra et al., 2007; Ruzich et al., 2015). Importantly, they also show high heritability (Hoekstra et al., 2007; Taylor et al., 2021) and are qualitatively similar and aetiologically linked to autistic traits in ASC (Lundström et al., 2012). Because of the variability of autistic traits in the general and the diagnosed populations, ASC may be viewed as an extreme of a neurodevelopmental continuum (Constantino & Todd, 2003).

Thus, studies targeting autistic traits can also inform clinical research. Moreover, including groups of participants with high autistic traits in research offers methodological benefits. For example, it facilitates recruiting a sample of sufficient size, controlling for comorbidities, and ensuring an appropriately matched control group (English et al., 2021). To capture autistic traits, several standardised tools have been developed. The most widely used one is the Autism Spectrum Quotient (AQ; Baron-Cohen, Wheelwright, Skinner, et al., 2001), followed by the Social Responsiveness Scale (Constantino & Gruber, 2005) and the Broad Autism Phenotype Questionnaire (Hurley et al., 2007)[3]. The AQ is a 50-item self-assessment questionnaire measuring the expression of autistic traits in an individual. In the initial publication, the mean score of the participants without ASC was 16, and only 2% of them scored 32 or higher, in comparison to 80% of the diagnosed group (Baron-Cohen, Wheelwright, Skinner, et al., 2001). Thus, although the AQ is not a diagnostic tool, it has a good discriminative validity as well as screening properties (Woodbury-Smith et al., 2005) and is sensitive to sub-clinical expressions of autistic traits (Hoekstra et al., 2007).

1.2.4 Social motivation hypothesis as a theory of autism

Since the first descriptions of autism in the 1940s (Kanner, 1943), a number of theories were proposed aiming to provide a model explaining the social difficulties in this condition (for an overview, see Bottini, 2018). Over the last decades, accounts identifying *social cognition* as the core deficit in ASC

[3] Based on Scopus citation count: 4836, 3826, 334, respectively (retrieved on 21/09/2021).

received extensive attention, followed by a more recent focus on *social motivation* (Dawson et al., 2002; Dawson, Webb, & McPartland, 2005; Grelotti et al., 2002). The *social motivation theory* encompasses these works and proposes that impairments in the social motivation mechanisms are the primary deficits in ASC, leading to abnormal social cognition and other social difficulties characteristic in this condition (Chevallier et al., 2012; Dawson et al., 1998; Mundy & Neal, 2000; Schultz, 2005).

Social motivation is a collection of psychological functions and biological mechanisms which equip us to operate in social environments through automatically orienting to social events (social orientation), pursuing and enjoying social interactions (social reward), and exerting effort to establish and preserve relations with others (social maintaining). Supporting the social motivation theory, there is behavioural evidence for impairments in all of the social motivation functions in autism (Chevallier et al., 2012). For example, individuals with ASC, compared to their neurotypical peers, fixate less on eyes and faces (Kirchner et al., 2011; Kliemann et al., 2010), and are less likely to re-engage in an interrupted collaboration (Liebal et al., 2008) or to use laughter for negotiating and maintaining social interactions (Hudenko et al., 2009).

It has been proposed that an underlying mechanism for those impairments in autism may be a reduced capability to represent the reward value of social stimuli (Dawson et al., 2002; Dawson, Webb, Wijsman, et al., 2005). As discussed, reward processing is a crucial component of human development. This is especially vivid in the social domain of rewards. A caregiver's feedback is a crucial signal for a child to learn which behaviours are socially appropriate and which are not: Positive feedback (e.g., smile or praise) reinforces appropriate behaviours, and negative feedback (e.g., frowned eyebrows or disapproving voice) decreases the chances that such behaviour would be repeated. If such reward-based learning was impaired, it would lead to a cascade of neurodevelopmental deficits: Diminished rewarding value of, for example, a smile, leads to less satisfaction from positive social interactions, which in turn entails diminished motivation for social situations, less experience with such, and, through lack of exposure and learning, social deficits.

The social motivation theory proposes that this is the mechanism leading to social deficits in ASC. Notably, alterations in reward function can also contribute to other symptoms of ASC, like development of restricted interests through enhanced pleasure linked to particular activities and objects (Dichter, Felder, et al., 2012; Dichter & Adolphs, 2012; Kohls, Yerys, et al., 2014). While

social rewards are claimed to have diminished reward value for individuals with autism, this is not the case for the non-social signals (the motivational deficits are suggested to be specifically manifested in the social domain). This theory generates a research hypothesis predicting that in experimental designs contrasting neuronal responses to social and non-social rewards, autism would be linked to lowered responsiveness to the first, but not the latter.

1.2.5 Conclusion: Autism

Autism is a neurodevelopmental condition characterised by social interaction impairments. On the sub-clinical level, autistic traits show similarities to the clinical symptomatology and are distributed normally in the general population. Our understanding of autism to date suggests a highly complex, heterogenous, and phenomenologically diverse condition manifesting in a range of symptoms with different levels of severity and potential various neuronal and aetiological bases. The social motivation theory proposes that social impairments in autism are a result of a cascade of developmental deficits caused by diminished rewarding value of social incentives in this population. Therefore, it is hypothesised that individuals with autism and with higher autistic traits display lower responsiveness to social rewards.

1.3 Reward responsiveness in autism

1.3.1 Empirical evidence regarding reward domain

Despite numerous empirical works testing the hypotheses generated by the social motivation theory, the results are inconclusive. Some studies, in support of the theory, report diminished neuronal or behavioural responses to the social rewards and typical responses to the non-social rewards in clinical autism (Benning et al., 2016; Cascio et al., 2014; Delmonte et al., 2012; Dubey et al., 2017; Gonzalez-Gadea et al., 2016; Kim et al., 2015; Lin, Rangel, et al., 2012; Ruta et al., 2017; Sasson et al., 2012; Scott-Van Zeeland et al., 2010; Sepeta et al., 2012; Silva et al., 2015; Stavropoulos & Carver, 2014b, 2014a) and in higher levels of autistic traits (Carter Leno et al., 2016; Cox et al., 2015; Dubey et al., 2015; Foulkes et al., 2015; Haffey et al., 2013; Rolison et al., 2017). At the same time, other studies suggest that autism and autistic traits are linked to either a more general reward impairment, i.e., diminished responsiveness to both social and non-social rewards (Baumeister et al., 2020; Kohls et al., 2011, 2013; Kohls, Thönessen, et al., 2014; Richey et al., 2014; Shafritz et al., 2015), no

impairment in either domain (Barman et al., 2015; Demurie et al., 2013, 2016; Ewing et al., 2013; Gilbertson et al., 2017; Neuhaus et al., 2015), or even enhanced neuronal responses to social signals (Dichter, Richey, et al., 2012; Pankert et al., 2014; van Dongen et al., 2015) and non-social rewards relating to circumscribed interests (Dichter, Felder, et al., 2012; Kohls et al., 2018; Pankert et al., 2014; Sasson et al., 2012; Watson et al., 2015) and other objects (Cascio et al., 2012; Dichter, Richey, et al., 2012; Groen et al., 2008).

This is further complicated by the fact that some studies directly compare social and non-social reward processing in the same sample, while others only include one domain. For example, some studies found no reward responsiveness impairment in ASC but they only utilised non-social incentives (Cascio et al., 2012, 2014; Greene et al., 2020; Larson et al., 2011; McPartland et al., 2012), so that no conclusions can be drawn about the potential reward deficit specific to the social domain. Moreover, studies using fMRI report evidence for both hyper- (Dichter, Richey, et al., 2012; van Dongen et al., 2015) and hypo-activation (Kohls et al., 2013; Scott-Van Zeeland et al., 2010) of reward-related brain structures in ASC. A recent meta-analysis of neuroimaging studies showed that there is accumulating evidence that autism is linked to atypical reward processing (Clements et al., 2018), which is further supported by literature reviews (Bottini, 2018; Keifer et al., 2021; Kohls et al., 2012; Neuhaus et al., 2010). However, among those reward-related structures for which group differences were found, some show hypo- (nucleus accumbens, bilateral caudate, anterior cingulate cortex, right insula) and some hyperactivation (left caudate, insula, putamen) in ASC (Clements et al., 2018). This is further complicated by the fact that the functional meaning of activation in these areas is still unclear. While hypoactivation in the reward structures is sometimes interpreted as an index of a functional deficit (Scott-Van Zeeland et al., 2010) other times it is attributed to higher efficiency in neuronal processing (Shafritz et al., 2015).

Despite the inconsistencies in the literature, the emerging pattern points to autism (and autistic traits) being linked to deficits in processing of especially social, and less non-social rewards (see Figure 1-2).

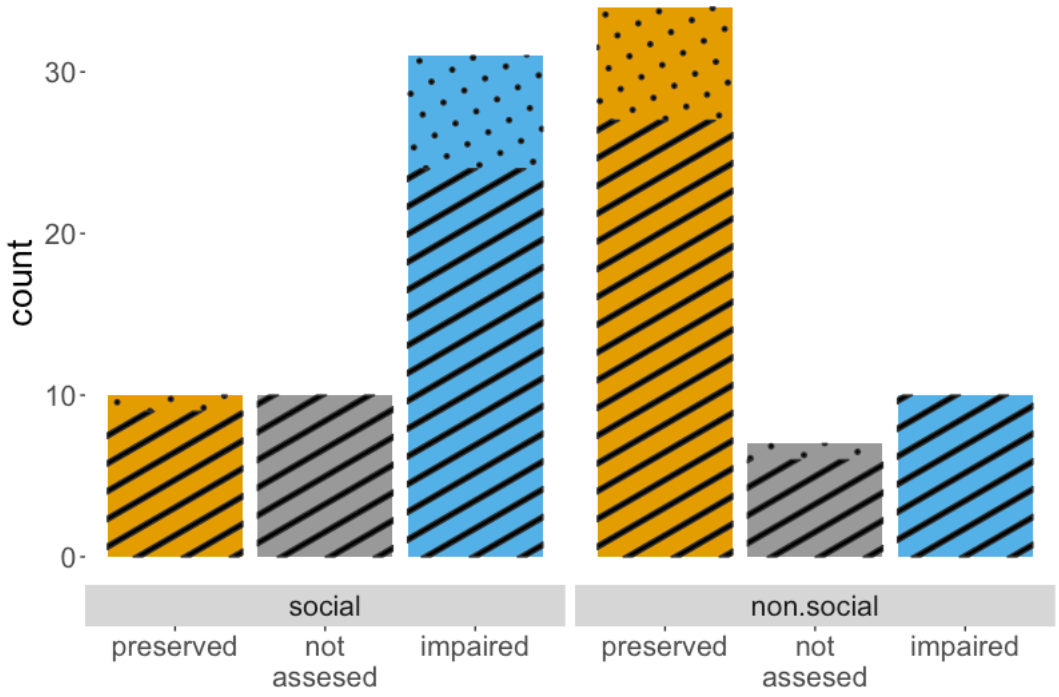

Figure 1-2 Number of empirical studies reporting preserved or impaired processing of social and non-social rewards in clinical autism (dashed) and autistic traits (dotted). Domain results labelled as "not assessed" include studies which utilised only rewards in the other domain. The database used in this plot includes 51 empirical studies investigating reward processing in autism mentioned in this chapter.

Linking atypical neuronal responses and socio-communicative impairments in autism may offer an interpretation of these results. However, while some studies find such links (Kohls et al., 2011; Schmitz et al., 2008), others fail to do so (Scott-Van Zeeland et al., 2010). Thus, it is not clear which direction of the deviations (stronger activation in ASC than control group, or vice versa) and in which brain structures could be considered a biomarker of deficiency in reward processing (Dichter, Damiano, et al., 2012). Moreover, opposing activation of the same structures in different studies produce null meta-analytic findings (Clements et al., 2018), which further complicates the big picture of reward processing in autism.

1.3.2 Empirical evidence regarding reward phases

There are accumulating data suggesting that autistic traits and clinical autism may be characterised by compromised reward anticipation in the social (Cox et al., 2015; Dichter, Richey, et al., 2012; Kohls et al., 2011; Stavropoulos & Carver, 2014a, 2014b) and non-social domains (Dichter, Felder, et al., 2012;

Dichter, Richey, et al., 2012; Kohls et al., 2011; Richey et al., 2014). While some studies also find preserved (Barman et al., 2015; Delmonte et al., 2012; Greene et al., 2020) or even enhanced (Groen et al., 2008; van Dongen et al., 2015) anticipation in these groups, an agreement for deficits in ASC in this reward phase has emerged (for reviews, see Keifer et al., 2021; Kohls et al., 2012). One promising explanation for this is functional disconnection of the structures within the reward circuitry in autism (Kohls et al., 2012). For example, there is evidence for altered functional connectivity during reward processing (Greene et al., 2020) and a reduced anatomical covariance between the fusiform and the amygdala (implicated in the processing of especially social rewards) in autism (Dziobek et al., 2010), as well as decreased functional connectivity within the fronto-striatal regions in higher autistic traits (Sims et al., 2013).

Literature concerning reward reception in autism is inconclusive (Kohls et al., 2012). There is empirical evidence for typical processing in ASC (Baumeister et al., 2020; Dichter, Richey, et al., 2012; Greene et al., 2020; Groen et al., 2008; Hulst et al., 2017; Larson et al., 2011; McPartland et al., 2012; Richey et al., 2014; van Dongen et al., 2015) as well as for impairments relative to social (Barman et al., 2015; Benning et al., 2016; Carter Leno et al., 2016; Delmonte et al., 2012; Gonzalez-Gadea et al., 2016; Rolison et al., 2017; Scott-Van Zeeland et al., 2010; Stavropoulos & Carver, 2014b) and non-social rewards (Dichter, Felder, et al., 2012; Schmitz et al., 2008).

A recent study (Baumeister et al., 2020) with a large sample (over 200 subjects with ASC) found autism-related striatal hypoactivation during social and non-social anticipation and no group differences in reception (descriptively the autism group showed hyperactivation in both domains, but this result did not survive corrections for multiple comparisons). In their meta-analysis, Clements and colleagues (Clements et al., 2018) found a hypoactivation during social anticipation, and hyperactivation during non-social anticipation and social reception. This analysis included only six studies because event-related designs are needed to disentangle reward phases but they are not always used in the fMRI studies (e.g., Kable & Glimcher, 2007; Kohls et al., 2013; Scott-Van Zeeland et al., 2010).

Similarly, behavioural studies are not specific in disentangling the reward phases. For example, reaction times or accuracy are an indirect measurement of the motivational value of incentives, but it is impossible to precisely extract 'wanting' and 'liking' from such designs. Moreover, absence of behavioural differences between ASC and control groups is often reported alongside

differences in neuronal processing (Baumeister et al., 2020; Greene et al., 2020; Kohls et al., 2013, 2018; Kohls, Thönessen, et al., 2014; Neuhaus et al., 2015; van Dongen et al., 2015), which suggests that behavioural markers may not be sensitive enough to capture reward atypicalities in this group. Although studies using EEG are suitable for filling this gap due to the high temporal resolution of this method, no meta-analysis has been so far conducted on the available data.

Together, although an emerging consensus is that autism is characterised mainly by deficiencies in reward anticipation, most of the empirical studies cannot provide direct evidence for the decoupled reward phases due to the experimental designs and methods (see Figure 1-3).

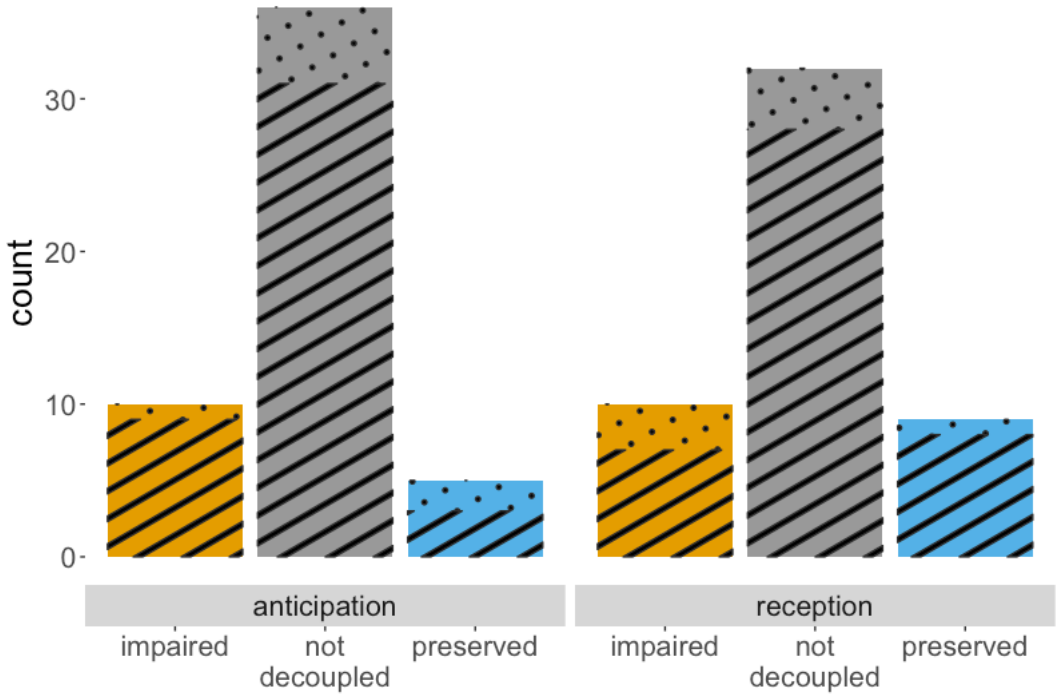

Figure 1-3 Number of empirical studies reporting preserved or impaired reward anticipation and reception of reward in autism (dashed) and autistic traits (dotted). Lebel "not decoupled" indicates studies which did not explicitly assess reward anticipation and reception separately. The database used in this plot includes 51 empirical studies mentioned in this chapter.

1.3.3 Social familiarity and anxiety

Given the particular focus on the social domain in autism, two additional factors should be incorporated in research: familiarity and social anxiety.

While the most common social rewards in empirical studies are faces, they are almost always faces that allow no further interaction, i.e., pictures of strangers not involved in the current situation. In contrast, in natural social situations, feedback is typically given by either familiar persons (e.g., a friend smiling in response to me telling a story) or unfamiliar individuals otherwise relevant in the current situation (e.g., a stranger frowning at me on a bus for listening to loud music). Nevertheless, no autism study has used exclusively familiar and/or relevant faces as social rewards (but see Hayward et al., 2018) for a design with a relevant social reward – the experimenter – in a sample of neurotypicals with varying autistic traits).

Crucially, observing faces of familiar and relevant persons elicits activation in the brain reward circuitry (Acevedo et al., 2012; Aron et al., 2005; Bartels & Zeki, 2004; Bayer et al., 2021; Ortigue et al., 2007). However, only a few studies have systematically addressed familiarity as a potential modulator of reward processing in autism (Neuhaus et al., 2015; Pankert et al., 2014; Stavropoulos & Carver, 2014a). They all included small samples sizes (less than 20 subjects in a group) in designs with group, familiarity, and domain (social and non-social) as factors. Moreover, in one study the faces were only incidental, i.e., additional to food rewards and not needed for feedback retrieval (Stavropoulos & Carver, 2014a). Nonetheless, one study showed decreased habituation of the electrodermal response for familiar faces (Neuhaus et al., 2015) suggesting differential processing of familiar and unfamiliar faces, albeit irrespective of autism diagnosis.

At the same time, there is evidence that otherwise aberrant processing of faces in autism is improved by familiarity (Pierce et al., 2004; Pierce & Redcay, 2008). This suggests that by using pictures of unfamiliar faces as incentives, studies may evoke a difference in neuronal processing between ASC and control groups, which could be attributable to lower-level face processing, instead of reward atypicalities. Thus, usage of familiar and/or relevant faces as social rewards may eliminate a perceptual confound in experimental designs.

Finally, the use of social feedback in experiments exposes the results to confounds related to social anxiety, which is characterised by autonomic reaction of anxiety to social situations, especially in fear of negative evaluation by others (Spain et al., 2018). Indeed, clinical SAD has been linked to deficient social reward anticipation and reception (Richey et al., 2014). Moreover, SAD is a common comorbidity of ASC (Bejerot et al., 2014; White et al., 2009) and is linked to reduced social motivation and poorer social skills in this group

(Spain et al., 2018). Therefore, due to the overlap between SAD and ASC, differences in reward processing between autistic and control groups may not be characteristic to autism, but at least partially result from the often-co-occurring anxiety. Indeed, comorbidities have been indicated as having the potential to explain contradictory results in clinical psychology (Bottini, 2018). Thus, social anxiety traits should be controlled for in experimental designs to eliminate this confound.

1.3.4 Conclusion: Reward responsiveness in autism

Although the emerging pattern of results from empirical studies suggests deficits associated with autism and autistic traits in the anticipation of particularly social rewards, the literature is mixed. Studies also find evidence for more general reward impairment, also in reception, and some report enhanced neuronal processing of rewards in this population. Moreover, studies rarely address some potentially crucial covariates in the social domain, like familiarity of rewards and comorbid social anxiety traits in autism. This striking discrepancy of results in the literature calls for a careful consideration of differences between studies in terms of their design, samples, and reward types. Identification of such discrepancies will help to understand the mixed results, interpret them, and improve future study designs.

2

Research aims

What are the aims of the research projects in this dissertation?

2. Research aims

Although it is of great importance to understand the nature and scale of reward responsiveness deficits in autism, the empirical results are so far mixed. The objective of this dissertation is to contribute to the literature with original work targeting the most important aspects which are inconsistently or scantily addressed in the field. In the following sections, based on the literature reviewed above, I identify these aspects and outlay the aims of the corresponding studies conducted in this dissertation. Finally, I introduce a theoretical analysis of rewards based on the insights and expertise acquired in this empirical work.

The overarching aim of this dissertation is to expound social and non-social reward processing with a special focus on autism and autistic traits using empirical evidence and a theoretical analysis.

2.1 Disentangling reward phases in autistic traits

There is accumulating evidence that aberrant reward processing is an endophenotype which cuts across diagnostic criteria of numerous psychiatric and neurodevelopmental disorders (Hyman, 2007). At the same time, a likely differentiating characteristic for different conditions is the pattern of atypicalities within the reward processing phases, i.e., anticipation and reception (Richey et al., 2014). Therefore, it is important to reliably describe the nature of reward processing deficits in autism regarding the possibly decoupled impairments of reward anticipation and reception.

The literature, albeit inconsistent (see section 1.3), points to aberrant reward anticipation rather than reception in autism and autistic traits (Keifer et al., 2021; Kohls et al., 2012). However, most of the published studies do not specifically dissociate the two phases due to the used methods and designs. The studies that investigate reward anticipation, focus on either its early or

late part, but in experiments reward anticipation stretches over a trial and it is likely to change over time (and thus, deficits may manifest in different stages).

Moreover, a growing number of studies report that sub-clinical autistic traits may modulate reward responsiveness in a similar way as in clinical ASC. Although such studies can inform autism research and offer several methodological benefits (e.g., attainability of participants), they are sparse. We conducted Study 1 to fill in these gaps and to empirically test the hypotheses generated by the social motivation theory, namely that higher levels of autistic traits are linked to deficits in anticipation and potentially in reception of social rewards.

The aim of Study 1 was to investigate the modulatory effects of autistic traits on early anticipation, late anticipation, and reception of social and non-social rewards.

We used a cued incentive delay task with social, monetary, and combined rewards. To eliminate the possibly confounding effect of aberrant processing of unfamiliar faces linked to autism, and to increase the rewarding value of the stimuli, we used a picture of a smiling face of the main experimenter as the social reward. In line with the social motivation theory (Chevallier et al., 2012), we hypothesised that higher levels of autistic traits would be associated with diminished amplitudes of the event-related brain potentials in response to social (a smile), but not non-social (money) rewards. Based on previous research (Kohls et al., 2011; Larson et al., 2011; McPartland et al., 2012; Richey et al., 2014; Stavropoulos & Carver, 2014b, 2014a), we expected to see this effect in early and late anticipation (indexed by the CNV) and in reception (measured with the P3). To our knowledge, we were the first to distinguish early and late anticipation in relation to autistic traits by measuring brain responses across all the reward phases.

Matyjek, M., Bayer, M., & Dziobek, I. (2020), Autistic Traits Affect Reward Anticipation but not Reception. *Scientific Reports 10*, 8396. doi: 10.1038/s41598-020-65345-x. This is an open access publication. The associated public repository includes the analysis code (https://osf.io/qwf2v/).

2.2 Reward responsiveness on the spectrum

Autism research is largely based on the psychopathological approach, i.e., the comparison between a clinical sample of individuals diagnosed with autism and a control group of individuals not meeting the diagnostic criteria. For this contrast to be comparable between studies, the control groups must be equally 'non-autistic'. However, a small but growing body of literature reports that autistic traits in the general population (i.e., the population-based approach) are linked to similar effects on reward processing as in clinically diagnosed autism. Therefore, while more empirical evidence is needed to draw firm conclusions about the role of subclinical autistic traits on reward responsiveness, it is important to carefully control for these traits in studies using the psychopathological approach.

The aim of Study 2 was to investigate anticipation and reception of social and non-social rewards in a sample of participants with autism and in neurotypical participants with varying levels of autistic traits.

We investigated ERP (the CNV and the SPN in early and late anticipation, the P3 in reception), pupillary, and behavioural (reaction times and ratings) responses to social (smiling face of the experimenter), monetary, and neutral (letters) outcomes in the cued incentive delay task. To provide a more complete picture of the role of autistic traits on reward processing in clinical autism and in the general population, we used both psychopathological (a group of subjects with low autistic traits vs. the ASC group) and population-based approaches (subjects with low vs. with high levels of autistic traits). Based on the results from Study 1 and the emerging literature (Bottini et al., 2018), and contrary to the social motivation hypothesis, we expected to see enhanced responses to both rewards in anticipation, and no group effects in the reception.

Matyjek, M., Bayer, M., & Dziobek, I. (in preparation for submission), Reward Responsiveness across Autism and Autistic Traits – Evidence from Neuronal, Autonomic, and Behavioural Levels. This study is pre-registered.

2.3 Familiarity and rewarding context

Even though familiar and personally relevant faces have a special standing in social cognition, elicit activation in the reward circuit (Acevedo et al., 2012; Aron et al., 2005; Bartels & Zeki, 2004; Bayer et al., 2021; Ortigue et al., 2007), and may be normally processed in autism (in contrast to non-familiar faces; Pierce et al., 2004; Pierce & Redcay, 2008), their role in reward responsiveness is yet to be explained. Moreover, while neuroimaging studies report enhanced neuronal processing of personal and relevant faces during passive observation, studies which specifically target reward processing usually employ an active task, i.e., participants must perform successfully to receive a reward. In the non-social domain it has been shown that 'active' rewards are considered more salient than 'passive' ones (Bjork & Hommer, 2007; Zink et al., 2004). Similarly, it is likely that 'active' smiling faces (shown after successful performance, like in Studies 1 and 2) are more rewarding than 'passive' ones, and that this may be further modulated by familiarity of the faces. Yet, empirical evidence is lacking.

The research aim of Study 3 was twofold: We aimed to investigate the modulatory effects of familiarity and of rewarding context on reward-related pupillary responses.

To this goal, we tested whether different levels of familiarity and relevance of smiling faces modulate pupil sizes. To distinguish processing of 'active' and 'passive' social rewards (i.e., the rewarding context), the same faces were shown in an active task (contingent on behaviour: delivered only in successful trials) and in a passive viewing task (delivered in absence of any action). We hypothesised that more familiar and more relevant faces, especially in the active task, would trigger larger pupil sizes, which would indicate higher rewarding and motivating values of these stimuli (Koelewijn et al., 2018).

Matyjek, M., Bayer, M., & Dziobek, I. (2021), Pupillary Responses to Faces are Modulated by Familiarity and Rewarding Context. *Brain Sciences 11*, 794. doi: 10.3390/brainsci11060794. This study is pre-registered and published with open access. The associated public repository includes data and analysis code (https://osf.io/623jg/).

2.4 Multidimensionality of rewards

A smile and money are two stimuli often used in empirical studies to reflect, respectively, a social and a non-social reward (as in Studies 1 and 2). However, there are more differences between them than the 'sociality' dimension. For example, smile is primary, and money is secondary. Because the two extremes of the primacy dimension can also be distinguished in terms of the neuronal activation they elicit (Levy & Glimcher, 2011), then significant differences in the brain responses to smile and money can be due to the sociality, due to primacy, or both. Hence, multidimensionality of rewards is a potential confound in research focusing on the sociality domain. Nevertheless, this is rarely discussed and addressed in experimental designs.

The aim of Study 4 was to systematically consider other dimensions of rewards than sociality.

In this perspective, the objectives were twofold. First, we aimed to raise awareness of the potential confounds in interpretation of the reported differences between social and non-social rewards if their multidimensionality is neglected. Second, we proposed a framework for future studies which would aid improvement of study designs.

Matyjek, M., Meliss, S., Dziobek, I., & Murayama, K. (2020), A Multidimensional View on Social and Non-social Rewards. *Frontiers in Psychiatry, 11*, 818. doi: 10.3389/fpsyt.2020.00818. This study is published with open access.

3

Original studies

This chapter includes three empirical studies and a theoretical perspective outlined previously.

3. Original studies

3.1 Study 1: Disentangling reward phases in autistic traits

Autistic Traits Affect Reward Anticipation but not Reception

Magdalena Matyjek, Mareike Bayer, & Isabel Dziobek

Abstract. Autism spectrum conditions (ASC) have been linked to aberrant reward processing, but it remains unclear whether it is a general dysfunction or limited to social stimuli, and whether it affects both phases of reward processing, namely anticipation and reception. We used event-related brain potentials and a population-based approach to investigate reward anticipation and reception to socially relevant (i.e., picture of experimenter's face showing approval/disapproval) and monetary rewards in 51 neurotypical individuals with varying levels of autistic traits. Higher autistic traits were associated with enhanced reward anticipation across reward types in the early anticipation phase (triggered by incentive cues), but not in the late anticipation phase (directly before reward reception), as reflected by the CNV component. The P3 component in response to reward reception showed a general increase for monetary outcomes, which was not modulated by autistic traits. These results suggest that higher autistic traits are related to enhanced reward anticipation, but do not modulate reward reception. No interaction between reward types and autistic traits was observed. We propose that the relevance of social rewards had higher reward value than commonly used pictures of strangers, which specifically normalised responses for individuals with high autistic traits.

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3.1.1 Introduction

Autism Spectrum Conditions (ASC) are characterised by persistent deficits in communication and social interactions (American Psychiatric Association, 2013). The social motivation account of ASC (Dawson, Webb, & McPartland, 2005; Schultz, 2005) suggests a decreased sensitivity and responsivity to social incentives (e.g. smiles) and consequently a diminished motivation for social interaction in individuals with ASC. Abnormal activation of the brain's reward system might cause children with ASC to appreciate and enjoy social stimuli less, which normally motivate typically developing children to interact (Chevallier et al., 2012). This lack of social motivation might lead to withdrawal from interactive situations, and therefore to deprivation of social and emotional input. In turn, insufficient exposure to interacting social environments might impair acquisition and development of communicative and social skills (Dziobek et al., 2010). The social motivation account proposes that social stimuli have lower rewarding power for individuals with ASC (Scott-Van Zeeland et al., 2010). However, this line of research was challenged by work showing general impairments in reward processing, which are not limited to the social domain (Kohls et al., 2011, 2013), and work showing no differences or even enhanced reward responsiveness in ASC (Dichter & Adolphs, 2012; Kohls et al., 2018; Pankert et al., 2014). Thus, so far it remains unclear whether a possible reward dysfunction in ASC is limited to the social domain, or manifests more generally.

One way to address this discrepancy in the literature is to use a population-based approach, in which individuals with ASC represent extreme values on the continuous distribution of autistic traits in the population (Constantino & Todd, 2003). Autistic traits are a set of personality characteristics that reflect the phenotypic expression of the genetic liability of autism (Hurley et al., 2007), and can be measured with questionnaires, like the Autism Spectrum Quotient (AQ; Baron-Cohen, Wheelwright, Skinner, et al., 2001). Both higher levels of autistic traits in a sub-clinical population and increased severity of autism symptomatology in ASC have been linked with abnormal reward processing (Carter Leno et al., 2016; Cox et al., 2015; Dichter, Richey, et al., 2012). Importantly, population-based studies inform psychopathological approaches (contrasting ASC-diagnosed vs. control subjects) by exploring reward processing within neurotypical groups. Neglecting heterogeneity of responsiveness to rewards in control groups can contribute to inconsistencies

in the literature (and stress the need for careful assessment of autistic traits in subclinical individuals).

Another notable factor when trying to explain inconsistencies in the literature is the nature of social stimuli used across studies. Even though there is evidence that social familiarity normalises face processing in ASC (Pierce et al., 2004), most studies have utilised pictures of strangers as social feedback, which may reduce the reward value of these stimuli, and thus decrease social motivation. Furthermore, social anxiety, which is a common comorbidity of autism (Bellini, 2006), may also influence reward responsiveness to social stimuli, as it is known to modulate face processing (Moser et al., 2008). Research concerned with reward processing in social contexts should therefore account for social relevance of the presented faces and face-processing biases linked to social anxiety.

Finally, reward processing comprises two distinctive phases, namely anticipation and reception (Berridge et al., 2009), which can be differentially affected in individuals with reward processing dysfunction, e.g. in addiction (Beck et al., 2009). Anticipation is the motivational, appetitive phase in which subjects seek and await reward. Usually the subsequent reception of reward is related to "liking" the outcome and experiencing pleasure. Research using electroencephalography (EEG) and neuroimaging is sparse and inconclusive about the pattern of possible reward processing impairments in autism, with studies reporting reduced processing only in anticipation of rewards or in both phases (e.g., (Dichter, Richey, et al., 2012; Richey et al., 2014) and (Dichter, Felder, et al., 2012; Stavropoulos & Carver, 2014b), respectively). Moreover, some studies (Gonzalez-Gadea et al., 2016; Kohls et al., 2011; Larson et al., 2011; McPartland et al., 2012; Schmitz et al., 2008) have targeted only one of the phases, thus providing only a partial picture of reward responsiveness.

To investigate anticipation and appreciation of rewards separately, a high temporal resolution technic is required. Event-related potentials (ERPs) – brain components extracted from the EEG signal – allow measuring brain responses with millisecond resolution, which is lacking in hemodynamic neuroimaging methods. ERPs have been effective in dissociating anticipation and reception in response to rewards in autism research, revealing atypical responses to anticipation (Cox et al., 2015; Groen et al., 2008; Kohls et al., 2011; Stavropoulos & Carver, 2014b) or reception (Carter Leno et al., 2016; Gonzalez-Gadea et al., 2016; Stavropoulos & Carver, 2014b) of rewards. Anticipatory

brain processes are reflected in the EEG signal as late negative potentials elicited at the central-parietal sites and associated with expectation of an upcoming stimulus, like the Contingent Negativity Variation (CNV; Grey Walter et al., 1964). The CNV amplitude has been reported to be modulated by motivation, effort, and the anticipation of affective or motivationally salient stimuli (Broyd et al., 2012). More elaborate, cognitive and affective stimulus processing is reflected in the P3 – a positive, centro-parietal component related to allocation of attentional resources. In the context of reward processing, it is believed to reflect the motivational significance of a reward (Wu & Zhou, 2009).

In this study we investigated the modulatory effects of autistic traits on reward anticipation and reception in social and non-social domains. We used a modified version of the cued incentive delay task (Knutson et al., 2000), with symbolic incentive cues indicating the type of outcome in a given trial. In order to achieve a more natural, real-life setting and to normalise possible differences in processing irrelevant faces linked to autistic traits, we used pictures of the main experimenter, i.e., a socially relevant interaction partner, as social reward stimuli. All participants met the experimenter for the first time on the day of the study and spent the same amount of time with her during the EEG preparations and verbal instructions for the tasks. This standardised exposure assured that the experimenter's familiarity was naturally built in the interaction. The shared social context and the importance of the experimenter in this situation were designed to make her face more socially relevant. In line with the social motivation account, we hypothesised that participants with higher levels of autistic traits (as measured with AQ) would display attenuated amplitudes of the CNV while anticipating social rewards (possibly also familiar faces; Stavropoulos & Carver, 2014a), than participants with low levels of autistic traits16. We hypothesised that autistic traits would modulate the reward reception measured with the P3 in the social, but not in the non-social condition (Carter Leno et al., 2016; McPartland et al., 2012).

To our knowledge no study has focused on the time course of anticipation, i.e., modulation of these responses in relation to early or late stages of anticipation in relation to autistic traits, which we targeted for an exploratory analysis in this study (Oumeziane et al., 2017).

3.1.2 Methods

3.1.2.1 Participants

55 volunteers participated in the study; the data sets of 4 participants were excluded due to poor EEG signal quality (1), inefficient language proficiency (1) and unreliable questionnaire data, i.e., inconsistent answer patterns (2). The remaining sample (26 women, 25 men) had a mean age of 27.8 years ($SD = 4.6$). Forty-eight participants were right-handed (Oldfield, 1971); all had normal or corrected-to-normal vision. All participants were recruited via flyers published on eBay Kleinanzeigen (a popular advertising platform in Germany) and distributed at Berlin's university campuses. Inclusion criteria were age (18–50), proficiency in German, no history of psychological, neurological, or psychiatric disorders in the last 6 months (including medication), and no past diagnosis of such. After the experiment, the aims of the study and the focus on autistic traits were revealed to the participants in a debriefing conversation. One participant reported then self-suspected autism with two diagnostic investigations in specialised autism diagnosis centres; both of which did not confirm a diagnosis of ASC. Participants were compensated 8 Euro per hour plus additional 4 Euro as a monetary reward earned during the task (for details, see section 3.1.2.2), which resulted in a total reimbursement of 20 Euro. All participants provided written informed consent; the study was approved by the ethics committee of the Faculty of Psychology of the Humboldt-Universität zu Berlin and was conducted in accordance with the Declaration of Helsinki.

3.1.2.2 Stimuli and task

Participants performed a cued incentive delay task, in which they had to guess the colour of a card drawn from a deck. For each correct response they received a reward – either a picture of a smiling face of the experimenter (a natural, relevant social reward), a monetary reward, or both combined. Participants were instructed about the task both in writing and verbally.

For an overview of the task, see Figure 3-1. In each trial, a cue (3×2.5 visual angles) indicating the reward type in a given trial was presented at the centre of the screen for 1000 ms. The cue was followed by a small white fixation cross (0.7×0.7 of visual angle) displayed centrally for 500 ms. Then, a blue and a purple card were displayed on both sides of the screen until the participant's response. Participants were instructed to make a guess about the colour of the

next card drawn from a deck consisting of blue and purple cards. Participants were required to press one of two response buttons indicating their choice (for the left and right card, respectively). The location (right or left) of the blue and the purple cards on the screen was random. There was no time constraint for the response. During the pre-feedback waiting period a fixation cross was presented for 1500 to 2000 ms (jittered across trials). A feedback stimulus (matching the incentive type indicated by the cue) was presented after the pre-feedback anticipation phase for 1000 ms.

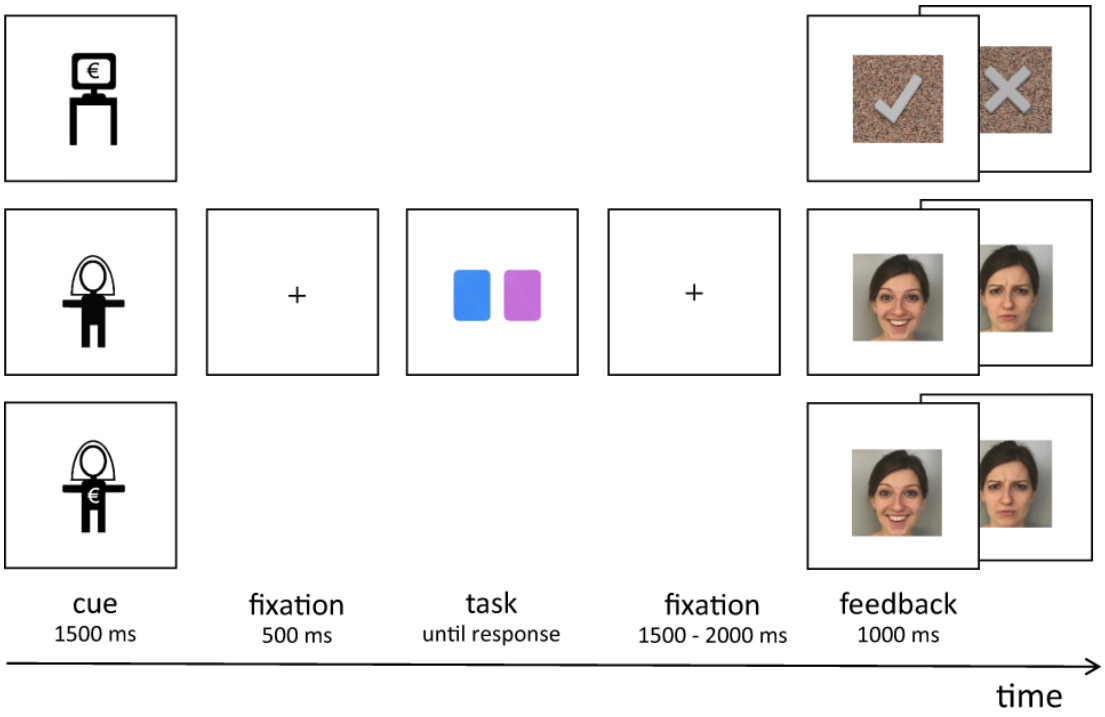

Figure 3-1 The cued incentive delay task with three conditions (from the top): monetary, social, and combined (social + monetary).

Three incentive conditions were introduced: social reward (S), monetary reward (M), and combined social + monetary reward (SM). Correct and incorrect responses in both the S and the SM condition were rewarded with a picture of a happy/approving or a disapproving face of the main experimenter, respectively. Participants were informed in the instructions that in the SM condition they received 5 cents as well as a smile and were aware of the respective conditions when engaging with the trials given the incentive cues that were provided. In the M condition, a symbol of a grey tick served as an indicator of the reward; an incorrect guess was followed by a grey cross. Both

symbols were displayed on a background made of scrambled pixels of the S rewarding feedback picture (the happy/approving face). All feedback stimuli were equal in size (3 ×3° of visual angle) and luminance. The feedback stimuli were presented in the centre of the screen for 1000 ms. Participants were instructed that in the M and the SM conditions each correct guess was rewarded with 5 cents. The current balance was displayed after each block. Participants were told that the study focused on decision making in game situations. However, in reality, participants' decisions were not influencing the feedback valence (to exclude the possible advantage of individuals with low intensity of autistic traits in learning an implicit rule; Nuske et al., 2013).

Altogether, 9 experimental blocks were presented pseudo-randomly. The first three blocks were of 10:18 proportion of reward to no-reward feedback. In the next three blocks the proportion changed to 14:14, and in the last three to 18:10. This grouping was designed to elicit a sense of agency and performance improvement over time in the participants (and eliminate possible frustration). Each group of three blocks consisted of one block for each incentive type (S, M, and SM; each block included only one type). The first 3 blocks were presented in random order. The next 2 groups of 3 blocks were presented in the same order as in the first 3 blocks. Each block consisted of 28 trials, resulting in 252 trials in total.

3.1.2.3 Procedure

After signing the consent form, participants were prepared for the EEG recording, during which time the experimenter maintained a light social conversation detailed by an interaction script. This was administered to achieve a natural familiarisation with the experimenter, with whom all participants spent the same amount of time and were exposed to various viewing angles of her face and her facial expressions. To emphasise the shared social context, the experimenter also pointed out that this study was her project and she cared for the participants' performance in the task. Then, participants were seated in a dimmed, electrically shielded room at a distance of 70 cm from a 19-inch computer screen. Participants were asked to place their chin and forehead on a head-rest in order to restrain movements.

After the recording, participants answered a number of debriefing questions and completed questionnaires displayed on a computer screen (see Questionnaires and debriefing questions). Then they were debriefed and informed about the real purpose of the study.

3.1.2.4 EEG data acquisition and pre-processing

The continuous scalp EEG was recorded from 64 silver/silver-chloride active electrodes (Biosemi Active Two) with a 512 Hz sampling rate. The electrodes were secured in an elastic cap according to the extended 10–20 international electrode placement system. Signals were referenced online to the CMS-DRL ground loop, which drives the average potential as close as possible to the amplifier zero. The electrode offsets were kept within the range of ± 20 microvolts. The horizontal and vertical electro-oculograms were acquired from four external electrodes, placed at the outer canthi and below both eyes. Two electrodes were additionally positioned on the left and right mastoids. The signals were filtered online with a 100 Hz low-pass and 0.01 Hz high-pass filter.

Offline, each signal was re-referenced to the average of all signals. Data were filtered with a low-pass filter of 40 Hz (slope 8 dB/oct). Channels with poor signals were interpolated using spherical splines of order 4 (0.1% of all channels). Continuous data were segmented into epochs ranging from −100 ms before to 7000 ms after the cue onset. All segments were referred to a 100 ms pre-cue baseline. An independent component analysis algorithm (restricted fast ICA) was used to identify and remove blinks and eye movements. Each segment was then further divided into three sub-segments related to the presentation of the incentive cue, the anticipation phase before the feedback, and the feedback. Respectively, the sub-segments were ranging from −100 ms before to 1500 ms after the cue onset; from −600 ms before feedback onset to feedback onset; and from −100 ms to 1000 ms after the feedback stimuli onset. We time-locked anticipatory responses to multiple events (cue and pre-feedback) to allow for a comparison of the CNV amplitudes across time, investigating how anticipation is built and sustained across the paradigm. A semi-automatic artifact rejection was applied to all epochs, excluding activations exceeding ± 100 microvolts or voltage steps larger than 100 microvolts. This led to rejection of 1.3% of trials for cue signals, 2.1% of trials for pre-feedback, and 0.8% for feedback signals. Across participants an average of 83 artifact-free trials was obtained in each condition for the cue responses (SM: $SD = 3.9$, M: $SD = 2.1$, S: $SD = 2.7$). Average number of pre-feedback segments was 82 in S and SM, and 83 in M (SM: $SD = 4.8$, M: $SD = 2.5$, S: $SD = 4.3$). For the feedback responses the average number of trials was 42 in each condition and reward/no-reward outcome (*SD*s for reward SM, S, and M, and no-reward SM, S, and M, respectively: 1.8, 1, 0.8, 1.9, 1.3, 1.2). Number of artifact-

free segments for cues, pre-feedback and feedback were not significantly different between conditions in each phase (all Fs < 1.15, ps > 0.32). Furthermore, the number of cue and pre-feedback segments did not differ significantly ($t = 1.92$, $p = 0.06$). Finally, epochs were averaged per subject, condition (S, M, SM) and separately for cues, pre-feedback, and feedback. All offline pre-processing steps were performed using BrainVision Analyzer (Brain Products GmbH, Munich, Germany).

3.1.2.5 Questionnaires and debriefing questions

All participants completed an online version of the Autism Spectrum Quotient (AQ; Baron-Cohen, Wheelwright, Skinner, et al., 2001) prior to the experiment. The AQ is a self-administered questionnaire assessing the degree of traits associated with autism in neurotypical individuals consisting of 50 items. In the original study evaluating the AQ, the control group scored on average 16.4 and the autism group 35.8 (Baron-Cohen, Wheelwright, Hill, et al., 2001). In this study participants' scores ranged from 6 to 35, with the mean of 18.3 ($SD = 7.3$). Females and males did not differ in their mean AQ score, $t(48.92) = -1.03$, $p = 0.31$.

After EEG recording, participants completed the Behavioural Inhibition and Approach Systems Scales (BIS/BAS; Carver & White, 1994), the Liebowitz Social Anxiety Scale self-reported (LSAS-SR; Liebowitz et al., 1985) and the Edinburgh Handedness Inventory (Oldfield, 1971).

The BIS/BAS questionnaire assesses two motivational systems, the behavioural activation system (BAS) and behavioural inhibition system (BIS). The BAS scale is further divided into 3 subscales: Drive, which assesses individual's inclination to pursue desired goals; fun seeking, related to the desire for new rewards and impulsive drive towards potential rewards; and reward responsiveness. The BAS is thought to be responsible for responding to incentives with positive affect and increased motivation. On the other hand, the BIS triggers experiences of anxiety, fear, and negative affect in response to threatening stimuli. Higher scores on both subscales are associated with higher sensitivity of the given system. Based on the previous literature (South et al., 2010, 2011) we expected autistic traits to be associated with higher BIS scores and lower BAS reward responsiveness subscale scores.

The LSAS-SR is a self-report scale assessing anxiety related to experiencing everyday social situations; higher scores indicate stronger anxiety. The

motivation for employing the LSAS-SR in the study were findings of modulatory effect of social anxiety on social reward processing (Cremers et al., 2015) and increased levels of social anxiety among population with autism (Bellini, 2006). We expected to see a positive correlation between the AQ and the LSAS-SR scores.

Additionally, participants answered the following debriefing questions: *How motivated were you to perform well in the experiment?* (general motivation); *Was the incentive type important to you?* (importance of condition); *Which reward was the most motivating one for you?* (motivational value of cues); *How rewarding did you find the feedback pictures?* (rewarding value of feedback).

3.1.3 Data analysis

All data analyses were performed using R ver. 3.4.3 (R Core Team, 2017). The significance level for all the tests was set to 0.05.

3.1.3.1 Brain responses

To assess potential effects of autistic traits and reward type on brain responses we utilised multiple regression analyses with mixed effects through the lmerTest package ver. 2.0.36 (Kuznetsova et al., 2017). Random intercepts for subjects were used in all multiple regression models based on improvement of Akaike's Information Criterion (Akaike, 1998) upon their addition to an intercept-only model. Random effects allow analysing hierarchical data while accounting for non-independence of the measures (Panasiti et al., 2016). Assumptions for multiple regression were checked for all models (normality, linearity, multicollinearity, homoscedasticity). Marginal and conditional R^2 were calculated as measures of goodness of fit for mixed models (Nakagawa & Schielzeth, 2013), in which marginal R^2 (R^2_m) reflects variance explained by fixed factors, and conditional R^2 (R^2_c) - variance explained by the entire model. The *p*-values were computed via Wald-statistics approximation (treating *t* as Wald *z*). To estimate a main effect of the incentive type, which is a multilevel categorical predictor, we administered an analysis of variance with Satterthwaite approximation for degrees of freedom and type II sums of squares on the regression models (Kuznetsova et al., 2017). Here we report only the significant effects, with Bonferroni-corrections where applicable. The complete regression tables including two contrasts (SM and M) are reported in the supplementary material. Since there is no established way of calculating standardised effect sizes for individual model terms in linear mixed models

due to the way the variance is partitioned (Rights & Sterba, 2018), see the supplementary material for all unstandardized slope estimates, which are the essential effect size statistics (Pek & Flora, 2018).

The temporal windows and regions of interest (ROI) for the CNV in response to cues and in the pre-feedback waiting period, and for the P3 in response to feedback, were chosen based on prior research and visual inspection of grand averages. The resulting time windows for anticipation phases (cue and pre-feedback) were the last 500 ms of each phase. For the cue this was calculated as 1000–1500 ms after cue onset (with −100 – 0 ms baseline). For the jittered pre-feedback the anticipation phase was time-locked to the onset of the feedback and defined as −500 – 0 ms (with −100 – 0 ms baseline locked to the onset of the pre-feedback fixation cross). The feedback P3 was identified from 300 to 500 ms after feedback onset. Mean amplitudes for these time windows were calculated from 9 electrodes for the CNV (CPz, CP1, CP2, Pz, P1, P2, POz, PO3, PO4) and from 9 electrodes for the P3 (Cz, C1, C2, CPz, CP1, CP2, Pz, P1, P2).

To explore the influence of autistic traits on brain responses we built multiple regression models with AQ score (continuous measure) and incentive type (S, M, SM) as the main predictors. To compare anticipatory responses across time, a model with additional phase (cue, pre-feedback) as a predictor was built. For the analysis of reward reception, AQ score, incentive type and outcome (reward, no-reward) were included. We controlled for social anxiety by including the LSAS-SR score in all the models.

3.1.3.2 Questionnaires and debriefing questions

The AQ, LSAS-SR and BIS/BAS scores were used as continuous measures of autistic traits, social anxiety, and approach/avoidance behaviour. All questionnaire scores were centred before including them in the models. Correlations between the questionnaires were computed using Pearson's rank correlation coefficients.

3.1.4 Results

3.1.4.1 ERPs

Anticipatory CNV amplitudes – cue and pre-feedback

We analysed attenuated anticipatory brain responses in relation to autistic traits by conducting a standard multiple regression analysis with the outcome variable of CNV amplitudes and predictor variables of autistic traits (AQ scores) and incentive type (S, M, SM). Figure 3-2 visualises the CNV values predicted by the models for both anticipation phases (early and late), with a median-split ($Mdn = 17$) of the sample into groups with high- and low autistic traits. The median-split was only used in the plots; all analyses were performed on continuous AQ score.

In the incentive cue phase, analysis of variance with Satterthwaite approximation for degrees of freedom and type II sums of squares on the regression model yielded a statistically significant effect of AQ, $F(1,51) = 4.81$, $p = .03$, and incentive type, $F(2,102) = 8.31$, $p < .001$. In the regression model, AQ predicted more negative CNV amplitudes with larger effects in SM ($est = -0.06$), than M ($est = -0.05$), than S ($est = -0.04$), but none of these contrasts survived corrections for multiple comparisons (corrected ps = .1, .14, .5, respectively). Pairwise contrasts of incentive types were statistically significant after correction only for SM vs. M ($est = -0.12$, $p < .001$), with the largest amplitudes for SM, followed by S and M.

In the pre-feedback phase the analysis of variance on the regression model showed statically significant effect only of the covariate, LSAS-SR, $F(1,51) = 5.02$, $p = .03$ (in regression $est = 0.03$ for all contrasts, corrected ps = 0.75).

Together, these results suggest that autistic traits are related to enhanced CNV amplitudes in response to an incentive cue indicating a future reward type. Unrelated to AQ, participants showed the largest responses to anticipation of the combined SM rewards. These effects disappear directly before reception of the reward (in the pre-feedback phase). Here, social anxiety seems to be inversely related to the CNV amplitudes.

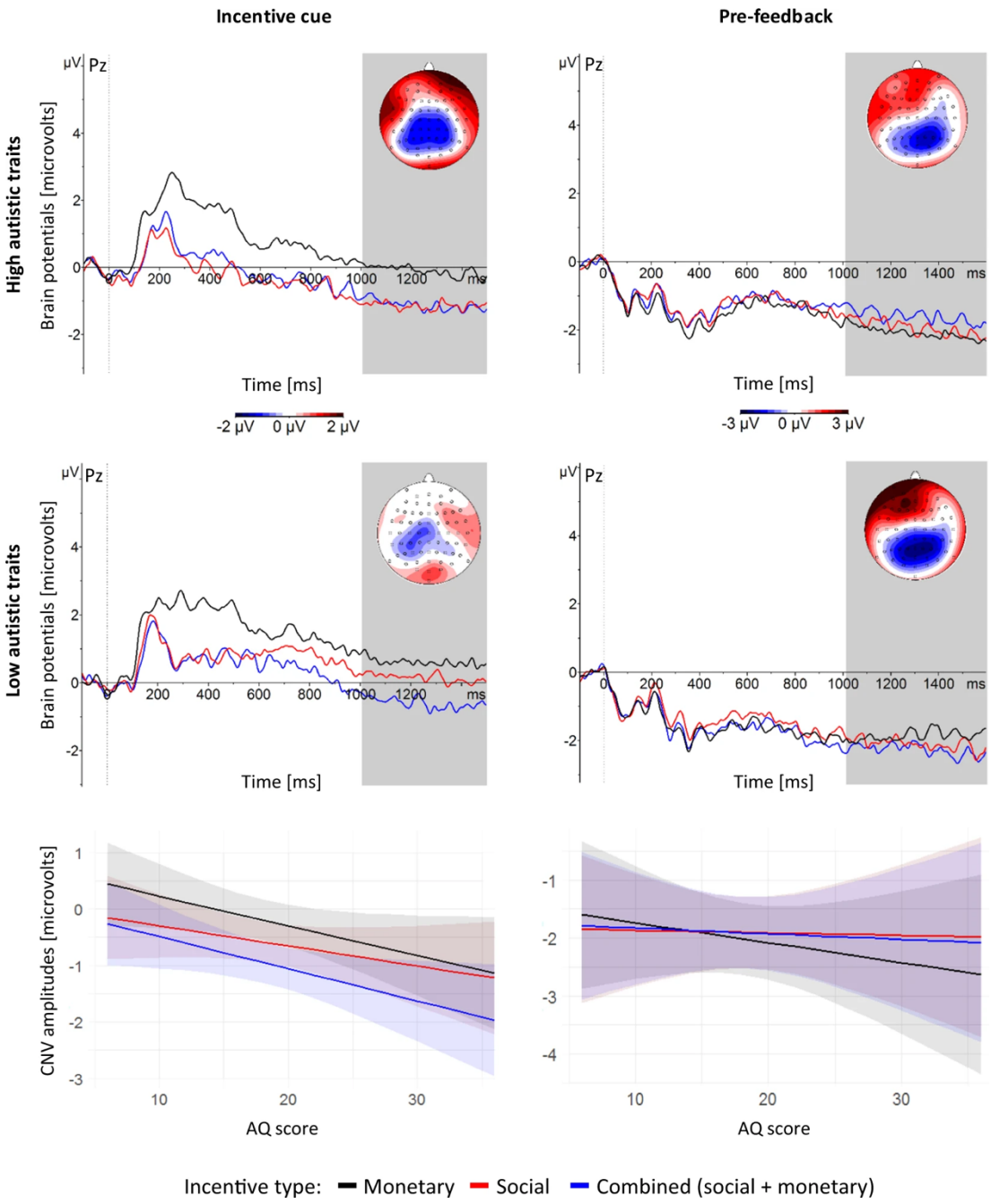

Figure 3-2 Top two rows: brain responses at the Pz electrode time-locked to the onset of the incentive cue (left side) and the pre-feedback waiting period (right side), averaged over participants with high- (top row) and low (middle row) autistic traits (based on a median-split, *Mdn* = 17). Topographic maps show scalp distributions at indicated time intervals. Note that pre-feedback CNV amplitudes are displayed here as locked to the onset of the waiting period, but were quantified for analyses relative to feedback onset, due to the variable lengths of the waiting period. Bottom row: mean predicted CNV amplitudes in the last 500 ms of the incentive cue presentation (left side) and the last 500 ms of the pre-feedback waiting period (right side). The shadowed bands indicate confidence intervals.

CNV responses across anticipation phases

To explore the CNV changes across anticipation phases, we built a model with the CNV as the outcome variable, AQ, incentive type and phase (cue, pre-feedback) as predictors, and LSAS-SR as a covariate.

Analysis of variance on this model yielded an interaction effect between autistic traits and phase, $F(1,255) = 7.57$, $p = .006$. The interaction between phase and AQ is presented in Figure 3-3. Autistic traits did not modulate the CNV in the pre-feedback phase. However, in response to incentive cues, autistic traits did indeed modulate the CNV, with higher trait levels eliciting larger amplitudes. This suggests that autistic traits play a greater role in early anticipation than in late reward anticipation.

The analysis of variance revealed also a main effect of phase, $F(1,255) = 66.94$, $p < .001$ (in the regression model the contrast of cue vs. pre-feedback also yielded a main effect of phase, with more negative CNV amplitudes in the pre-feedback, with the largest effect in M ($est = 1.8$, smaller in S ($est = 1.3$), and the smallest in SM ($est = 0.93$); for all contrasts corrected ps $< .003$), and LSAS-SR, $F(1,51) = 4.44$, $p = .04$ (in regression, ests $= 0.02$ across contrasts; corrected ps $= .11$). Since LSAS-SR was utilised as a covariate and phase showed a significant interaction effect with another predictor, these two main effects were no longer investigated.

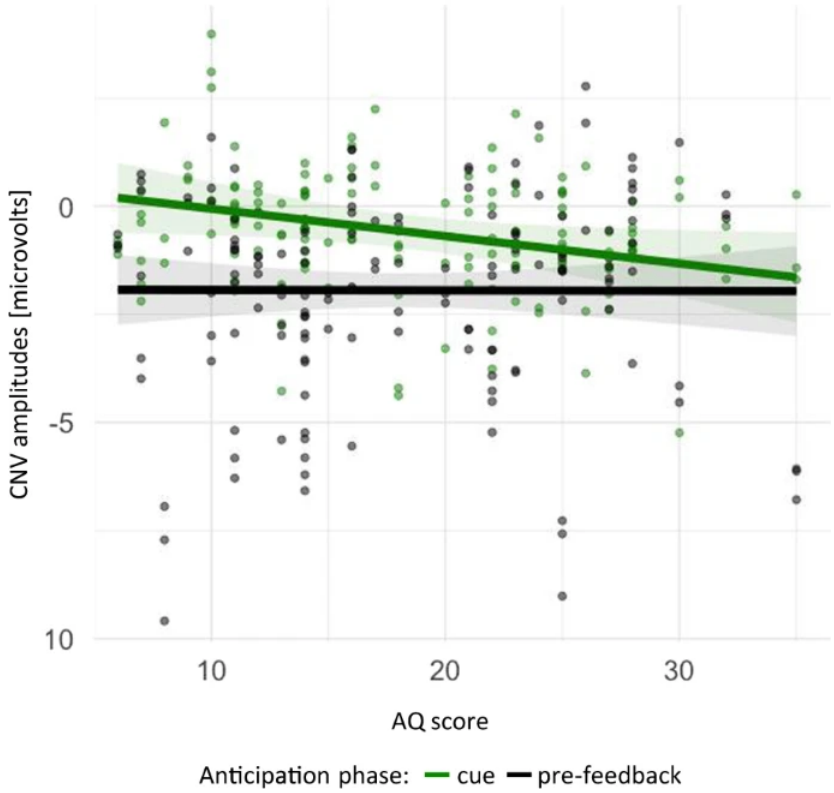

Figure 3-3 Mean predicted CNV amplitudes for AQ scores in both anticipation phases (negative CNVs indicating enhanced anticipation). The shadowed bands indicate confidence intervals.

The P3 amplitude in response to feedback

To explore the brain responses during feedback processing, a multiple regression model was built with P3 amplitudes as the dependent variable, AQ, incentive type and outcome (reward, no reward) as predictors, and LSAS-SR as a covariate.

Analysis of variance of this model revealed a significant main effect of reward type, $F(2,255) = 44.21$, $p < .001$, and regression results confirmed statistically significant differences for S vs. M ($est = 1.25$) and S vs. SM ($est = 1.3$; for both contrasts corrected $ps < .001$). P3 responses to SM and M were statistically indistinct ($est = -0.05$, corrected $p > 1$). The analysis of variance also revealed a main effect of outcome (reward vs. no-reward), $F(1,255) = 10.2$, $p = .002$, with larger P3 amplitudes for reward outcomes ($ests = 0.39–0.43$ across contrasts, all corrected $ps >= .18$).

Figure 3-4 shows the significant effects revealed in the analysis of variance administered to the model. Rewards elicited larger P3 amplitudes than no rewards. Both M and SM triggered larger responses than S.

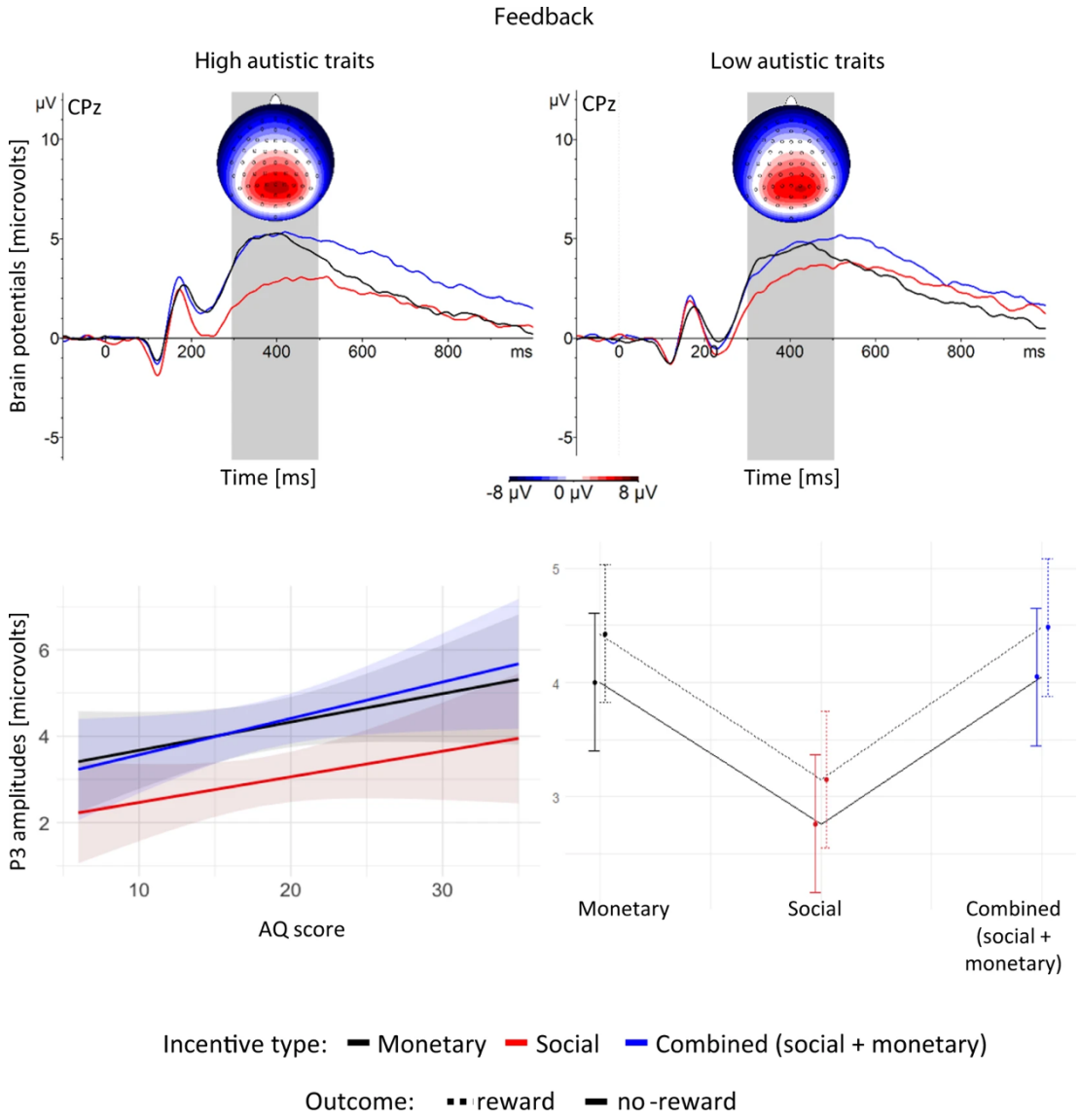

Figure 3-4 Top row: brain responses at electrode CPz, time-locked to the onset of feedback, averaged over participants with high- (left panel) and low (right panel) autistic traits (based on a median-split, *Mdn* = 17). Topographic maps show the scalp distributions across conditions at indicated time intervals. Bottom row: mean predicted P3 amplitudes for 300–500 ms after feedback onset across the AQ scores (left panel) and across incentive type and outcome (right panel). The shadowed bands indicate confidence intervals and the error bars show standard error.

3.1.4.2 Behavioural data

Questionnaires

We found statistically significant correlations between AQ scores and LSAS-SR ($r = 0.38$, $p = .006$), BIS scale ($r = 0.54$, $p < .001$), BAS reward

responsiveness scale ($r = -0.29$, $p = .04$), and BAS fun seeking scale ($r = -0.3$, $p = .03$). The correlation between AQ and BAS drive scores showed a trend effect ($r = -0.27$, $p = .06$). Together, these results point at the relation of higher autistic traits and increased social anxiety, higher sensitivity of the inhibition system, and weaker responsiveness to anticipation or occurrence of rewards. Altogether, these results suggest that individuals with high autistic traits are motivated stronger by avoidance of punishment than by drive to rewards.

3.1.4.3 Debriefing questions

Participants with high and low autistic traits did not differ in their general self-reported motivation during the experiment, $t(48.1) = -1.35$, $p = .18$, nor in the ratings of motivational power of incentive cues, $\chi^2(2) = 2.01$, $p = .37$, or in perceived importance of incentive types, $\chi^2(1) = 0$, $p = 1$. Autistic traits were also unrelated to subjective reward values of the social ($r = -0.13$, $p = .36$), or non-social feedback pictures ($r = 0.07$, $p = .61$). Altogether, autistic traits did not influence any self-reported behavioural measures.

3.1.5 Discussion

This study used a modified version of a cued incentive delay task with socially relevant faces to explore brain sensitivity to social, monetary, and combined social-monetary rewards in neurotypical participants with varying levels of autistic traits. We observed enhanced early anticipation of rewards in high autistic traits when triggered by symbolic, incentive cues representing possible outcomes of the conditions, as reflected in the CNV amplitudes. The brain responses were largest when anticipating the combined (social and monetary) rewards, independently of autistic traits. All these effects disappeared in late anticipation, i.e., directly before the reception of rewarding/non-rewarding feedback. A secondary analysis revealed an interaction effect of AQ scores and anticipation phase, suggesting that autistic traits were associated with increased anticipation during the early phase (triggered by a symbolic incentive cue), but did not modulate the responses in the late anticipation phase (directly before reward reception). Appreciation of received rewards reflected in higher P3 amplitudes was the largest for monetary and combined outcomes across levels of autistic traits.

Contrary to our hypotheses, our data do not support the predictions of the social motivation account, as we did not observe any interactions of autistic traits and reward types. However, a recent systematic review (Bottini, 2018)

examined 27 studies out of which 15 did and 12 did not support the social motivation hypothesis, which suggests that our results are not incidental. The heterogeneity of results reported so far calls for more research to examine the underlying mechanisms of social and non-social reward processing in autism and autistic traits, which are not yet well explained. Moreover, our results have to be considered in the light of the experimental design: One of its goals was to increase ecological validity of social stimuli by introducing pictures of the main experimenter, who was a relevant interaction partner, whereas most other studies used faces of strangers (Delmonte et al., 2012; Kohls et al., 2011, 2013; Scott-Van Zeeland et al., 2010; Sepeta et al., 2012; Stavropoulos & Carver, 2014b). Our choice was based on reports of reduced activity of the fusiform face area in individuals on autism spectrum in response to pictures of strangers, but not familiar faces (Pierce et al., 2004) and normalised pupillary responses to familiar, but not to strangers' faces (Nuske et al., 2014).

Atypical processing of faces has also been observed across autistic traits (Stavropoulos et al., 2018). The CNV amplitude in the early anticipation was indeed modulated by the incentive type, with incentives with social components reaching larger amplitudes than the solely monetary one. Therefore, it seems likely that presenting familiar (all participants recognised the person in the stimuli pictures as the experimenter prior to the task) and socially relevant (the experimenter and the participants shared a social context, in which the experimenter was an important interaction partner) stimuli might have normalised responsiveness to social reward in participants with higher levels of autistic traits. Even though, it is important to keep in mind that a single smiling face on a computer screen does not mimic natural social interactions, as faces in such situations are always seen in a complex context.

However, by using a familiar and relevant face we aimed to increase the ecological validity while maintaining both high experimental control and comparability to the large body of existing studies using smiling faces as rewards. So far, two studies directly compared familiar vs. unfamiliar faces in reward-based paradigms. One of them (Stavropoulos & Carver, 2014a) used faces as incidental rewards (co-occurring with food rewards), which made them redundant for retrieving the feedback valence information and does not allow independent assessment. Since processing of the faces was not task-relevant, the results of this study cannot be compared directly to our design, in which processing of the faces was crucial for retrieving both rewarding and informative values of the feedback. In the second study (Pankert et al., 2014)

children with ASC benefited more than the control group from both familiar and unfamiliar social (as well as non-social) rewards, as measured with reaction times and false alarms rates. This suggests increased reward responsiveness in the ASC group, which is in line with our finding of enhanced reward anticipation in higher autistic traits. However, to our knowledge no study to date has investigated familiarity effects across autistic traits. It is possible that brain responses to irrelevant (unfamiliar) social stimuli differ between individuals with high and low autistic traits when such stimuli convey informative feedback and reward. Although this should be addressed in a study specifically targeting this question, this interpretation of our results suggests that the relevance of social stimuli might modulate social motivation.

Alternatively, interaction effects of incentive types and autistic traits could have been unobserved in our data because such modulations might not manifest in subclinical levels of autistic traits. However, previous studies have documented the interaction effects in neurotypical samples varying in levels of autistic traits before (Carter Leno et al., 2016; Cox et al., 2015) and have further shown associations for a range of other cognitive and emotional characteristics that are relevant to autism (Foulkes et al., 2015; Haffey et al., 2013; Puzzo et al., 2010; Stavropoulos et al., 2018), which makes this an unlikely explanation for our pattern of results. Therefore, we favour the interpretation that the use of socially relevant faces in our study normalised the reward responsiveness to social rewards across autistic traits.

We observed that higher autistic traits were associated with stronger CNV responses to incentive cues of all reward types. The CNV is believed to reflect expectation of an upcoming event, and to be modulated by motivation and anticipation of affective stimuli (Broyd et al., 2012). Our results suggest that higher autistic traits were linked to larger anticipatory activation reflecting forming of reward representations in response to incentive cues. Though autism has primarily been linked to reduced reward anticipation (Dichter, Felder, et al., 2012; Kohls et al., 2011; Stavropoulos & Carver, 2014b), some findings have been reported that are in line with our results. One study (Pankert et al., 2014) observed greater behavioural responsiveness of autistic than control children to reward contingencies, given their baseline at a no-reward condition. Other studies observed larger anticipatory ERP amplitudes in children with autism than in a control group when expecting positive feedback (and non-social reward; Groen et al., 2008), and increased activation of multiple brain areas (i.e., nucleus accumbens and hippocampus to monetary

incentives; amygdala and insular cortex to social incentives) in ASC during reward processing (Dichter, Richey, et al., 2012). An alternative explanation of our results, which do not match the majority of findings on the topic, could be that larger CNV amplitudes represent arousal for the upcoming task performance, rather than reward anticipation (Brunia et al., 2012). However, observed differences between reward types, with the strongest responses to the incentive of combined (social and monetary) reward, make this unlikely. Such pattern rather suggests an additive motivating value of the social and monetary reward incentives, and adds to the interpretation of the CNV amplitudes as an indicator of reward anticipation.

Neither AQ nor reward type effects manifested in the pre-feedback waiting period directly preceding reward reception, despite visible anticipatory brain responses occurring in this time-window in the form of the CNV. The secondary analysis of anticipation over time yielded an interaction effect of AQ scores and anticipation phase, revealing that autistic traits affected processing in the early anticipation stronger than in the late one. Further, reward anticipation as indexed by the CNV was overall stronger in the late phase, albeit not influenced by either reward type or autistic traits.

To our knowledge, this study is the first one to investigate the early phase of reward anticipation in the context of autism. We used abstract representations of possible future rewards as incentive cues, triggering early anticipation of rewards. Oftentimes studies used the same stimulus (typically a smiling face) as both an incentive cue, which communicates a future possible reward, and as a feedback stimulus serving as the obtained reward (Cox et al., 2015; Kohls et al., 2011). This confounds reward anticipation and reward reception, making it impossible to interpret responses to cues as solely reflecting reward anticipation. This is especially important in paradigms comparing processing of social versus monetary rewards. Symbolic monetary outcomes (e.g., a picture of a coin) usually indicate future reception of a tangible reward (cash reimbursement). Social feedback typically consists of a smiling face, which is in itself a transient, immediate reward. Using a smiling face as an incentive cue is supposed to only indicate a future rewarding smiling face, which is later delivered with the same stimulus. Hence, in such designs reward anticipation cannot be interpreted, as it indeed includes reward reception. To extract the anticipation unaffected by prematurely delivered reward, we utilised symbolic representations of the rewards. Time-locking brain potentials to the onset of symbolic incentive cues in this study revealed modulatory effects of autistic

traits (larger responses in high traits) and reward types (the largest responses for the combined social and monetary incentives). This suggests that the incentive cues indeed elicited representations and anticipation of future rewards, as reflected in the occurrence of an anticipatory CNV component.

This sensitivity to cue – reward associations in higher autistic traits regardless of reward type was unexpected and stands at odds with accounts proposing impaired forming of stimulus-reward associations in autism resulting in decreased reward anticipation (Dawson et al., 2001). Since reward sensitivity is essential for conditioning processes and reinforcing appropriate behaviours (leading, in turn, to successful social interactions), it is crucial to understand the reasons for mixed results reported in the literature. One explanation could be that the atypical pre-feedback processing in participants with high autistic traits found in other studies (Cox et al., 2015) does not result from an inability to build stimulus-outcome associations, but rather reflect differences in the time course of reward anticipation between high and low autistic traits. Considering the CNV amplitudes in the early and late stages of reward anticipation in our paradigm, high autistic traits seem to be linked to more stable responses over time – not diminished directly before reward reception, but rather enhanced when triggered by incentive cues. In contrast, low autistic traits were associated with increasing anticipation over time – less anticipation than for high autistic traits in response to incentive cues, but increasing shortly before receiving the feedback and rewards, resulting in comparable reward anticipation for high and low autistic traits directly before reward reception. It is not clear what drives this difference in trajectory between low and high traits. Perhaps forming representations of rewards based on abstract cues is facilitated in higher levels of autistic traits. Possibly other inter-individual features in individuals with higher autistic traits in our sample, like anxiety or increased sensitivity to punishment (reflected in statistically significant correlations between AQ and LSAS-SR / BIS scores, respectively), modulated the processing shortly before outcome reception, refraining further excitation of the reward system. Altogether, our findings of increased responses in early but not late anticipation of rewards associated with high autistic traits demonstrate that targeting neuronal mechanisms underlying early responses to abstract representations of rewards offer new insights into reward sensitivity in autism.

We observed that the P3 component was elicited in response to feedback stimuli. The P3 amplitudes were larger for the monetary and the combined

(social + monetary) conditions, than for the social condition. Since the social and combined rewards consisted of the same stimuli, the different brain responses to them imply that participants were aware of the reward type indicated by the preceding symbolic incentive cues. This provides further evidence that incentive cues successfully elicited reward representations. There is no evidence for social and monetary rewards being additive, as both the combined and the monetary-only outcomes elicited similar responses: participants seem to have appreciated the monetary component when both accompanied and unaccompanied by social appreciation (preference for monetary rewards has been observed in neurotypicals before; Kohls et al., 2009, 2011). Since the P3 has been previously shown sensitive to reward magnitude and valence (Goldstein et al., 2006; Wu & Zhou, 2009), the data suggest a preference for tangible rewards over transient ones, at least in experimental settings.

Interestingly, differences across autistic traits and reward types were only visible in neuronal responses. Self-reported motivational and rewarding values of incentive cues and rewards did not differ between participants with low and high autistic traits. Hence, the brain responses in this study add to the growing body of literature stressing sensitivity of ERPs to cognitive and affective processes which may not manifest in behaviour (Cox et al., 2015; Kohls et al., 2011).

Our study contributes to autism research by investigating autistic traits in a population-based approach, and to the existing literature on reward responsiveness by proposing a novel insight into dynamics of anticipation over time (across paradigm phases). By using pictures of a socially relevant interaction partner as reward stimuli we aimed to provide an experimental context better resembling natural social situations. Our finding of enhanced early but not late reward anticipation in high autistic traits offers a new insight into the dynamics of reward processing in the context of the autism spectrum. It also demands a more refined interpretation of the social motivation account and its predictions about aberrant (multi)dimensional responsiveness to rewards in autism.

Moreover, this study offers a population-based view, in which neurotypical participants vary in levels of autistic traits and individuals diagnosed with autism would represent the extreme levels of these traits. Our results of autistic traits modulating reward anticipation stress the need for a careful control of neurotypical groups serving as controls for autism spectrum subjects in

psychological research. Apparent heterogeneity of sub-clinical (control) populations in terms of reward responsiveness may contribute to explaining mixed results in the literature exploring differences in reward sensitivity between individuals with and without autism.

Finally, targeting various stages of reward processing (early and late reward anticipation, reward reception) allows a more fine-grained characterisation of functional and dysfunctional reward processing. Since functional disconnection of reward processing phases has been observed in other groups with reward processing dysfunctions (addicts; Balodis & Potenza, 2015), it can also have implications for autism. Identifying atypical stages of reward responsiveness in autism can facilitate personalised therapies by selectively targeting the vulnerable sub-processes, which in turn are likely to reinforce desired therapy effects (Insel et al., 2010).

3.1.6 Supplementary material

Notes:

Est = estimate

CI = Confidence Intervals

σ^2 = within group variance

τ 00 = between group variance

ICC = Interclass Correlation (the ratio of the between-cluster variance to the total variance)

AIC model/null model = Akaike Information Criterion of the model in discussion or the null model (containing only intercept as a predictor) P-values were computed via Wald-statistics approximation (treating t as Wald z), uncorrected.

preFDB = prefeedback

Table 3-1 Regression results for the CNV in response to cues

	CUE: CNV									
Predictors	*Est.*	*SE*	*CI (0.95)*	*t*	*p*	*Est.*	*SE*	*CI (0.95)*	*t*	*p*
Intercept	-0.98	0.18	-1.33 – -0.62	-5.36	**<0.001**	-0.22	0.18	-0.58 – 0.14	-1.21	0.225
LSAS-SR	0.01	0.01	-0.01 – 0.02	0.76	0.446	0.01	0.01	-0.01 – 0.02	0.76	0.446
AQ	-0.06	0.03	-0.11 – -0.00	-2.15	**0.032**	-0.05	0.03	-0.10 – -0.00	-1.98	**0.048**
SM - M	0.75	0.19	0.39 – 1.12	4.08	**<0.001**					
SM - S	0.38	0.19	0.01 – 0.74	2.03	**0.042**					
M - S						-0.38	0.19	-0.74 – -0.02	-2.05	**0.040**
AQ : SM - M	0.00	0.03	-0.05 – 0.05	0.17	0.864					
AQ : SM - S	0.02	0.03	-0.03 – 0.07	0.84	0.402					
AQ : M - S						0.02	0.03	-0.03 – 0.07	0.67	0.505

Random Effects		**Model Information**	
σ^2	0.87	Observations	153
$\tau_{00\ code}$	0.82	Marginal R^2 / Conditional R^2	0.108 / 0.540
ICC_{code}	0.48	AIC_{model} / $AIC_{null\ model}$	499.513 / 535.919

Table 3-2 Regression results for the CNV in the pre-feedback phase

	PRE-FEEDBACK: CNV									
Predictors	*Est.*	*SE*	*CI (0.95)*	*t*	*p*	*Est.*	*SE*	*CI (0.95)*	*t*	*p*
Intercept	-1.91	0.31	-2.52 – -1.30	-6.15	**<0.001**	-2.03	0.31	-2.64 – -1.42	-6.55	**<0.001**
LSAS-SR	0.03	0.01	0.00 – 0.06	2.24	**0.025**	0.03	0.01	0.00 – 0.06	2.24	**0.025**
AQ	-0.01	0.05	-0.10 – 0.08	-0.21	0.831	-0.03	0.05	-0.12 – 0.06	-0.75	0.455
SM - M	-0.12	0.19	-0.50 – 0.26	-0.62	0.532					
SM - S	0.00	0.19	-0.38 – 0.39	0.03	0.980					
M - S						0.13	0.19	-0.25 – 0.51	0.65	0.516
AQ : SM - M	-0.02	0.03	-0.08 – 0.03	-0.91	0.361					
AQ : SM - S	0.01	0.03	-0.05 – 0.06	0.20	0.841					
AQ : M - S						0.03	0.03	-0.02 – 0.08	1.11	0.265

Random Effects		**Model Information**	
σ^2	0.96	Observations	153
$\tau_{00\ code}$	3.95	Marginal R^2 / Conditional R^2	0.085 / 0.821
ICC_{code}	0.80	AIC_{model} / $AIC_{null\ model}$	587.013 / 695.147

Table 3-3 Regression results for the CNV in two phases – cue and pre-feedback

	CUE and PRE-FEEDBACK: CNV									
Predictors	*Est.*	*SE*	*CI (0.95)*	*t*	*p*	*Est.*	*SE*	*CI (0.95)*	*t*	*p*
Intercept	-0.98	0.26	-1.48 – -0.48	-3.81	**<0.001**	-0.23	0.26	-0.73 – 0.28	-0.88	0.380
LSAS-SR	0.02	0.01	0.00 – 0.04	2.11	**0.035**	0.02	0.01	0.00 – 0.04	2.11	**0.035**
AQ	-0.07	0.04	-0.14 – 0.00	-1.95	0.052	-0.07	0.04	-0.14 – 0.00	-1.83	0.067
SM - M	0.75	0.28	0.20 – 1.31	2.66	**0.008**					
SM - S	0.38	0.28	-0.18 – 0.93	1.32	0.186					
M - S						-0.38	0.28	-0.94 – 0.18	-1.33	0.182
cue - preFDB	-0.93	0.28	-1.48 – -0.37	-3.26	**0.001**	-1.80	0.28	-2.36 – -1.25	-6.34	**<0.001**
AQ: SM - M	0.00	0.04	-0.07 – 0.08	0.11	0.911					
AQ : SM - S	0.02	0.04	-0.06 – 0.10	0.55	0.585					
AQ : M - S						0.02	0.04	-0.06 – 0.09	0.43	0.664
AQ : cue - preFDB	0.08	0.04	0.00 – 0.15	1.97	**0.049**	0.05	0.04	-0.03 – 0.13	1.23	0.217
SM - M : cue - preFDB	-0.88	0.40	-1.66 – -0.09	-2.18	**0.029**					
SM - S : cue - preFDB	-0.37	0.40	-1.16 – 0.42	-0.92	0.356					
M – S : cue - preFDB						0.51	0.40	-0.28 – 1.29	1.26	0.208
AQ : SM - M : cue - preFDB	-0.03	0.06	-0.14 – 0.08	-0.52	0.603					
AQ : SM - S : cue - preFDB	-0.02	0.06	-0.12 – 0.09	-0.29	0.773					
AQ : M - S : cue - preFDB						0.01	0.06	-0.10 – 0.12	0.23	0.817

Random Effects		**Model Information**	
σ^2	2.05	Observations	306
$\tau_{00\ code}$	1.32	Marginal R^2 / Conditional R^2	0.176 / 0.498
ICC_{code}	0.39	AIC_{model} / $AIC_{null\ model}$	1199.097 / 1303.481

Table 3-4 Regression results for the P3 in response to outcomes

	FEEDBACK: P3									
Predictors	*Est.*	*SE*	*CI (0.95)*	*t*	*p*	*Est.*	*SE*	*CI (0.95)*	*t*	*p*
Intercept	4.08	0.31	3.47 – 4.68	13.26	**<0.001**	4.03	0.31	3.42 – 4.63	13.10	**<0.001**
LSAS-SR	-0.01	0.01	-0.04 – 0.01	-0.88	0.378	-0.01	0.01	-0.04 – 0.01	-0.88	0.378
AQ	0.09	0.05	0.00 – 0.18	2.00	**0.046**	0.07	0.05	-0.01 – 0.16	1.66	0.097
SM - M	-0.05	0.22	-0.49 – 0.39	-0.22	0.823					
SM - S	-1.30	0.22	-1.74 – -0.86	-5.79	**<0.001**					
M - S						-1.25	0.22	-1.69 – -0.81	-5.56	**<0.001**
no-reward – reward	0.43	0.22	-0.01 – 0.87	1.93	0.054	0.42	0.22	-0.02 – 0.86	1.87	0.062
AQ: SM - M	-0.02	0.03	-0.08 – 0.05	-0.49	0.622					
AQ : SM - S	-0.03	0.03	-0.09 – 0.03	-1.09	0.276					
AQ : M - S						-0.02	0.03	-0.08 – 0.04	-0.60	0.551
AQ : no-reward – reward	-0.01	0.03	-0.07 – 0.05	-0.38	0.701	-0.02	0.03	-0.08 – 0.04	-0.60	0.548
SM - M : no-reward – reward	-0.01	0.32	-0.63 – 0.61	-0.04	0.968					
SM - S : no-reward – reward	-0.04	0.32	-0.66 – 0.58	-0.13	0.894					
M – S : no-reward – reward						-0.03	0.32	-0.65 – 0.59	-0.09	0.927
AQ : SM - M : no-reward – reward	-0.01	0.04	-0.09 – 0.08	-0.15	0.878					
AQ : SM - S : no-reward – reward	0.02	0.04	-0.07 – 0.10	0.40	0.688					
AQ : M - S : no-reward – reward						0.02	0.04	-0.06 – 0.11	0.56	0.579

Random Effects		**Model Information**	
σ^2	1.28	Observations	306
$\tau_{00\ code}$	3.53	Marginal R^2 / Conditional R^2	0.118 / 0.766
ICC_{code}	0.73	AIC_{model} / $AIC_{null\ model}$	1119.680 / 1391.224

3.2 Study 2: Reward responsiveness on the spectrum

Reward Responsiveness across Autism and Autistic Traits – Evidence from Neuronal, Autonomic, and Behavioural Levels

Magdalena Matyjek, Mareike Bayer, & Isabel Dziobek

Abstract. Deficits in processing of social rewards have been suggested to lie at the root of social impairments in autism spectrum conditions (ASC). While evidence for atypical reward function in ASC is mounting, it remains unclear whether these abnormalities manifest specifically in hypo- or hyper-responsiveness and in the social domain or more generally. Moreover, stimuli used as social rewards in studies often lack familiarity and relevance, which are known to enhance reward-related responses. In this study, we investigated behavioural (reaction times and ratings), neuronal (event-related potentials), and autonomic (pupil sizes) responses to three conditions – relevant social rewards, money, and neutral informative outcomes – in 26 ASC and 53 neurotypical subjects varying in levels of autistic traits, as measured with the Autism Spectrum Quotient (AQ). We used both a population-based approach (low AQ (LAQ) vs. high AQ (HAQ)) and a psychopathological approach (LAQ vs. ASC) to investigate the effects of both sub-clinical and clinical autistic traits on reward responsiveness. As hypothesised and preregistered, using relevant social context, we observed that the behavioural, neuronal, and autonomic responses in ASC and HAQ were no differently influenced by condition than in LAQ. Moreover, regardless of the condition, ASC in contrast to LAQ showed enhanced brain responses (the CNV) in early anticipation and larger pupil constrictions in reward reception. Both effects were also predicted by the AQ. Further, ASC showed typical performance (reaction times) and rated the stimuli's motivational and rewarding values lower than the other groups. Our results do not offer evidence for specifically social reward deficits in ASC. Instead, the data suggest enhanced neuronal and autonomic reward responsiveness linked to autism with simultaneously typical performance and reduced self-reported motivational and rewarding values of stimuli. Together, these results emphasise the need to investigate multiple processing levels for a broader picture of reward responsiveness in ASC.

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3.2.1 Introduction

Rewards constitute a crucial factor in learning (Schultz, 2015) and thus are immensely important for life. The social motivation theory suggests that responsiveness to rewards in autism spectrum conditions (ASC) is abnormal at least in the social domain (Chevallier et al., 2012). The consequence of this could be a cascade of neurodevelopmental difficulties including reduced pleasure from interacting with others, withdrawal from social situations, insufficient exposure to social stimuli, and finally social interaction deficits. Thus, it was suggested that deficits in reward responsiveness may lie at the root of social impairments in autism (Dawson et al., 2002; Dawson, Webb, Wijsman, et al., 2005).

Importantly, this account is based on observations that behavioural manifestations of altered social motivation (e.g., lower orienting towards social stimuli) are linked to reduced activation of the reward circuit, like the amygdala and the orbitofrontal cortex (Chevallier et al., 2012). Thus, hypo-responsiveness to rewards (quantified as hypoactivation of the reward circuit (Baumeister et al., 2020), diminished electrical brain activity (Kohls et al., 2011), decreased autonomic responses (Sepeta et al., 2012), slower reactions (Demurie et al., 2011), etc.) was speculated to be the underlying cause for the well-documented decreased behavioural motivation for social stimuli in autism (Chevallier et al., 2012). The first formulations of the social motivation theory predicted that reward responsiveness is deficient in ASC especially in the social domain (Dawson et al., 2002; Dawson, Webb, & McPartland, 2005; Schultz, 2005) but more recent works suggest general abnormalities in this group, manifesting in both social and non-social domains (Bottini, 2018; Clements et al., 2018; Keifer et al., 2021; Kohls et al., 2012).

However, the empirical studies testing the predictions of the social motivation theory have yielded mixed results. While some published works report that ASC is related to hypo-responsiveness to specifically social (e.g., Scott-Van Zeeland et al., 2010; Sepeta et al., 2012; Stavropoulos & Carver, 2014b, 2014a) or both social and non-social rewards (e.g., Baumeister et al., 2020; Kohls et al., 2011, 2013; Kohls, Thönessen, et al., 2014; Richey et al., 2014), other studies find no differences between ASC and control groups (e.g., Demurie et al., 2016; Ewing et al., 2013; Gilbertson et al., 2017). Moreover, some studies report *hyper*-responsiveness to rewards in ASC, especially to objects related to circumscribed interests (e.g., Cascio et al., 2014; Kohls et al., 2018; Watson et

al., 2015), but also to other social and non-social rewards (e.g., Matyjek, Bayer, et al., 2020; Pankert et al., 2014; van Dongen et al., 2015). Similarly, a recent meta-analysis of neuroimaging studies found both hypo- and hyper-activations in the reward brain circuit in the ASC group in comparison to control individuals (Clements et al., 2018). However, while any difference between the ASC population and control groups may be considered atypical, both enhanced and attenuated reward-related responses are not sufficient or clear evidence to support the claims of the social motivation theory.

To interpret these mixed results, neuronal abnormalities should be linked to behavioural manifestations of social impairments in ASC (yet, evidence for this link is often lacking; Baumeister et al., 2020; Kohls et al., 2013; Scott-Van Zeeland et al., 2010). Capturing indexes of reward responsiveness on multiple levels (e.g., neuronal and behavioural) has the potential to inform the interpretation of conflicting results in the literature and provides a more complete picture of the process. Although several indexes of reward responsiveness have been investigated in the past research in the context of autism, including behavioural (e.g., reaction times, effort, accuracy; Demurie et al., 2011; Ewing et al., 2013; Geurts et al., 2008), neuronal (neuroimaging and electroencephalography (EEG); e.g., Kohls et al., 2011; Scott-Van Zeeland et al., 2010), and autonomic (e.g., electrodermal activity, pupil sizes; Neuhaus et al., 2015; Sepeta et al., 2012) levels, to our knowledge no study to date has collected responses from all three levels from the same sample in a reward-related paradigm. In the current study, we fill in this gap by reporting behavioural indexes of reward responsiveness (ratings of motivational and rewarding values of stimuli as well as combined measures of reaction times and accuracy), event-related potentials (ERPs), which offer excellent temporal resolution allowing for separate estimations of reward processing phases: anticipation and reception (Berridge, 1996, 2009; Berridge et al., 2009), and pupillary responses, which reflect the neuronal activation in the locus coeruleus (LC), a structure vastly involved in reward processing and motivation (Aston-Jones et al., 1999; Bast et al., 2018; Bouret & Richmond, 2015).

Together, although the social motivation theory has attracted considerate attention thanks to the potential to explain autistic symptomatology, the heterogenous results and the unclear connection between neuronal correlates of reward responsiveness and behavioural symptoms of autism have casted doubts on its validity. This emphasises the importance to investigate reward responsiveness on multiple processing levels and calls for a consideration of

the methodological aspects of experimental designs in the available studies (Bottini, 2018).

For example, even though autistic traits in the general population have been repeatedly related to atypicalities in reward processing (Carter Leno et al., 2016; Cox et al., 2015; Dubey et al., 2015; Matyjek, Bayer, et al., 2020; Rolison et al., 2017; Sims et al., 2013), studies contrasting ASC and neurotypical individuals rarely control for autistic traits in the latter. Importantly, autistic traits are distributed normally across the general population (Baron-Cohen, Wheelwright, Skinner, et al., 2001; Hoekstra et al., 2007; Ruzich et al., 2015), they are aetiologically linked to autistic traits in ASC, and they seem to assess the same latent constructs in ASC and non-clinical samples (Lundström et al., 2012). Thus, studying effects of autistic traits on reward responsiveness in subclinical populations could assist in identifying relevant phenomena for ASC. Moreover, at least some of the inconsistencies in the literature investigating reward processing in autism may be due to the level of autistic traits in the control groups, as neglecting them may render it difficult to compare group effects between studies. Therefore, to provide a broader picture of reward processing in the autism spectrum, in the current study we investigated it using both *population-based* and *psychopathological* approaches, i.e., we compared individuals with low levels of autistic traits (and no autism diagnosis) to those with high levels of the traits (and no diagnosis), and to individuals diagnosed with autism.

Further, important but rarely addressed aspects in processing of social rewards are familiarity and social relevance of the persons providing the feedback (and rewards) in an experiment. A common social reward stimulus in studies is a smiling face of an unknown person, who is irrelevant in the study situation. However, familiar and relevant faces are rated as more rewarding and elicit higher activation in reward-related brain structures (Acevedo et al., 2012; Bayer et al., 2021; Matyjek, Bayer, et al., 2021; Sugiura, 2014). Moreover, familiarity of faces has the potential to improve otherwise aberrant face processing in ASC (Pierce et al., 2004; Pierce & Redcay, 2008). For these reasons, as social rewards in this study, we used pictures of the smiling face of the main experimenter: a familiar and relevant in the context person (also see Hayward et al., 2018; Matyjek, Bayer, et al., 2020). Finally, because our design included facial expressions indicating successful or unsuccessful performance in a trial, it was important to address social anxiety traits in the participants, as anxious individuals are especially sensitive to social

evaluation (Spain et al., 2018). Moreover, social anxiety is a common comorbidity of autism (Bejerot et al., 2014; Bellini, 2006) and has been previously linked to deficient reward processing (Cremers et al., 2015; Richey et al., 2014). Therefore, we planned to control for the modulatory effects of social anxiety traits on reward responsiveness.

In this modified design with a socially relevant context, we expected that the familiar social stimuli would normalise reward-related responses in individuals with high levels of autistic traits and autism. Thus, on all processing levels (neuronal, autonomic, and behavioural), we expected to observe similar anticipation and reception of social, monetary, and neutral incentives across diagnostic groups and autistic traits (Barman et al., 2015; Demurie et al., 2013, 2016; Ewing et al., 2013; Gilbertson et al., 2017; Neuhaus et al., 2015). Further, conforming to the results from a similar study design of our group (Matyjek, Bayer, et al., 2020) and in line with work of other groups (Pankert et al., 2014; van Dongen et al., 2015), we expected to observe enhanced neuronal and autonomic responses in individuals with ASC and high levels of autistic traits in contrast to those with low trait levels. Because the available research suggests that ASC-specific atypicalities in reward responsiveness are more pronounced in the anticipation than reception phase (Keifer et al., 2021; Kohls et al., 2012), and our previous results identified differences between early and late phases of reward anticipation, we further expected that these group differences would be stronger in early than in late anticipation (Matyjek, Bayer, et al., 2020), but would not be observed in reception (Bottini, 2018). Finally, in order to confirm that the targeted responses are reward-related, we predicted to see larger responses to rewarded conditions (social and monetary) in all measures, as compared to the neutral outcomes (Cox et al., 2015; Kohls et al., 2011).

Additionally to testing these primary hypotheses, we aimed to explore several secondary analyses. First, to further quantify behavioural indexes of reward responsiveness, we collected scores estimating inhibition and approach tendencies from the participants and aimed to relate them to the neuronal and autonomic measures as well as autistic traits. Second, although we were primarily interested in *reward* responsiveness and for that the primary analyses were conducted on the data from successful trials (where reward could be obtained), we also planned to explore the neuronal and autonomic responses in the reception of unsuccessful (non-rewarded) trials. Finally, for a dimensional analysis of autistic traits (instead of group-based), we explored whether the trait levels across all participants predict the reward-

related reaction times, ERPs, and pupillary responses in linear and non-linear models.

Overall, this study set out to investigate behavioural, neuronal, and autonomic responses in anticipation and reception of monetary and relevant social rewards as well as neutral outcomes across individuals with different levels of autistic traits and with autism.

3.2.2 Methods

The methods, hypotheses, and analyses were preregistered at https://osf.io/3re72. Data, analysis code in R, and an html file including all analyses steps and results can be found at https://osf.io/vse38/.

3.2.2.1 Sample size determination

To estimate the sample size, we performed a power analysis with the g*power software (Faul et al., 2009), with power set to 0.8 and with an intermediate effect size f = 0.302. The effect size was calculated from the between-subject factor of group (high vs. low autistic traits) in response to reward cues in our previous experiment (Matyjek, Bayer, et al., 2020). This analysis yielded a total sample size of 52 with 26 data sets in each of two groups planned for comparisons (ASC vs. low autistic traits, and high vs. low autistic traits). Based on this, we planned to recruit 26 participants per group, summing up to the total of 78 participants.

3.2.2.2 Participants

A total of 82 volunteers across three groups (ASC, low- and high autistic traits) participated in the study. The data sets of 3 participants (two from the ASC group) were excluded due to poor EEG signal quality (1), refusal to perform a task involving money (1), and a technical issue with EEG recording (1). Demographic information for all groups with group comparisons are summarised in Table 3-5. All participants provided written informed consent; the study was approved by the ethics committee of the Faculty of Psychology of the Humboldt-Universität zu Berlin and was conducted in accordance with the Declaration of Helsinki. After the experiment, the aims of the study were revealed to the participants in a debriefing conversation. Participants were compensated 8 Euro per hour plus additional 4 Euro as a monetary reward

earned during the task (for details, see section 3.2.2.3), which resulted in a total of 30-40 Euro.

Neurotypical participants

Neurotypical participants were recruited via internet advertising platforms and flyers distributed at Berlin's university campuses. Inclusion criteria were age (18-50), proficiency in German, no history of psychological, neurological, or psychiatric disorders in the last 6 months (including medication), and no past diagnosis of such. Interested volunteers were asked to complete the Autism Spectrum Questionnaire (AQ; Baron-Cohen, Wheelwright, Skinner, et al., 2001) and were invited to participate based on the score (we aimed to increase the spread of the scores and to balance the size of low and high scoring groups). The mean AQ score in the neurotypical group (N = 53) was 18.6 (SD = 8.7); groups with high (HAQ) and low (LAQ) autistic traits (N = 25 and 26, respectively) were created based on a median split (Mdn = 17). This sample (30 females and 23 males) had a mean age of 31.3 (SD = 9.3). All participants had normal or corrected-to-normal vision and 50 were right-handed (based on the Edinburgh Inventory, Oldfield, 1971). One participant reported attending a psychotherapy in the last six months, and two more earlier than that. No participants in this group had been medicated with psychopharmaceuticals.

ASC group

Participants with ASC were recruited via an Autism outpatient clinic of the Charité— Universitätsmedizin Berlin, the Specialized Outpatient Clinic for Social Interaction, University Outpatient Clinic for Psychotherapy and Diagnostics of the Humboldt-Universität zu Berlin, an online forum for ASC community (www.aspies.de), and internet advertising platforms. All participants were confirmed to have a prior diagnosis matching the DSM-5 autism spectrum disorders (American Psychiatric Association, 2013) made by professionals in specialised autism-diagnosis centres (the diagnosis was confirmed directly by the centres and/or by a written diagnosis provided by the participants). In subjects with available additional diagnostic information (16), diagnoses were confirmed additionally with the Autism Diagnostic Observation Schedule (ADOS; Lord et al., 2000), and for 12 of those patients also with the Autism Diagnostic Interview Revised (ADI-R; Bölte & Poustka, 2001; Lord et al., 1994), a semi-structured interview administered to the caretakers. Additionally, inclusion criteria were age (18-50) and proficiency in German. All

participants had normal or corrected-to-normal vision and 20 participants were right-handed. Several participants in the ASC group reported experiencing a psychological illness (all depression and/or anxiety) or attending a psychotherapy in the last six months (N=6), and earlier (N=5). Four participants were medicated at the time of the study or in the last six months and two more earlier than that (all with selective serotonin or serotonin-norepinephrine reuptake inhibitors).

Table 3-5 Demographic and trait characteristics of subject samples in all groups. Count is provided for gender and means (with standard deviations) for all other items. HAQ = high autistic traits, LAQ = low autistic traits, ASC = Autism Spectrum Disorder, AQ = Autism Spectrum Quotient score, BIS/BAS = Behavioural Inhibition/Approach System, LSAS-SR = Liebowitz Social Anxiety Scale, R:N/L = Right, Neutral/Left (handedness), OR = odds ratio in Fisher's Exact Test. Statistically significant tests were marked with ** for p < .01 and *** for p < .001.

Group description			
	LAQ *N* = 26	HAQ *N* = 27	ASC *N* = 26
Gender – female:male	18:8	12:15	13:13
Age (years)	30.6 (7.9)	31.9 (10.6)	32.7 (10.7)
AQ (total)	10.9 (2.3)	25.9 (5.5)	39.3 (5)
BAS drive	12.5 (2.1)	11.6 (1.9)	11.2 (2)
BAS reward responsiv.	16.8 (1.7)	15.7 (2.3)	14.9 (2.3)
BAS fun seeking	12.5 (1.8)	11.2 (1.9)	9.7 (2.7)
BIS	18.8 (3.2)	20.9 (4.7)	23.5 (3.8)
LSAS-SR	31.1 (15.9)	58.6 (27.2)	83.5 (32.2)
Handedness – R:N/L	25:1	25:2	20:6
Between-group differences			
	LAQ vs. HAQ	LAQ vs. ASC	
Gender	*OR* = 2.76	*OR* = 2.21	
Age (years)	*t* = -0.51	*t* = -0.79	
AQ (total)	*t* = -13.02***	*t* = -26.25***	
BAS drive	*t* = 1.71	*t* = 2.35*	
BAS reward respons.	*t* = 1.87	*t* = 3.42***	
BAS fun seeking	*t* = 2.68*	*t* = 4.43***	
BIS	*t* = -1.93	*t* = -4.93***	
LSAS-SR	*t* = -4.51***	*t* = -7.42***	
Handedness	*OR* = 0.51	*OR* = 6.25	

3.2.2.3 Stimuli and task

We adapted a cued incentive delay task (Knutson et al., 2000) to include both social and non-social rewards. Participants were shown a cue indicating a possible reward in a given trial and asked to speedily respond to a following

target. For correct responses they received either a reward – a picture of the experimenter's smiling face (social reward) or money (5 cents, non-social reward), or a reward-neutral outcome (an informative letter). Figure 3-5 depicts the overall course of a trial. The instructions were delivered both in writing and verbally.

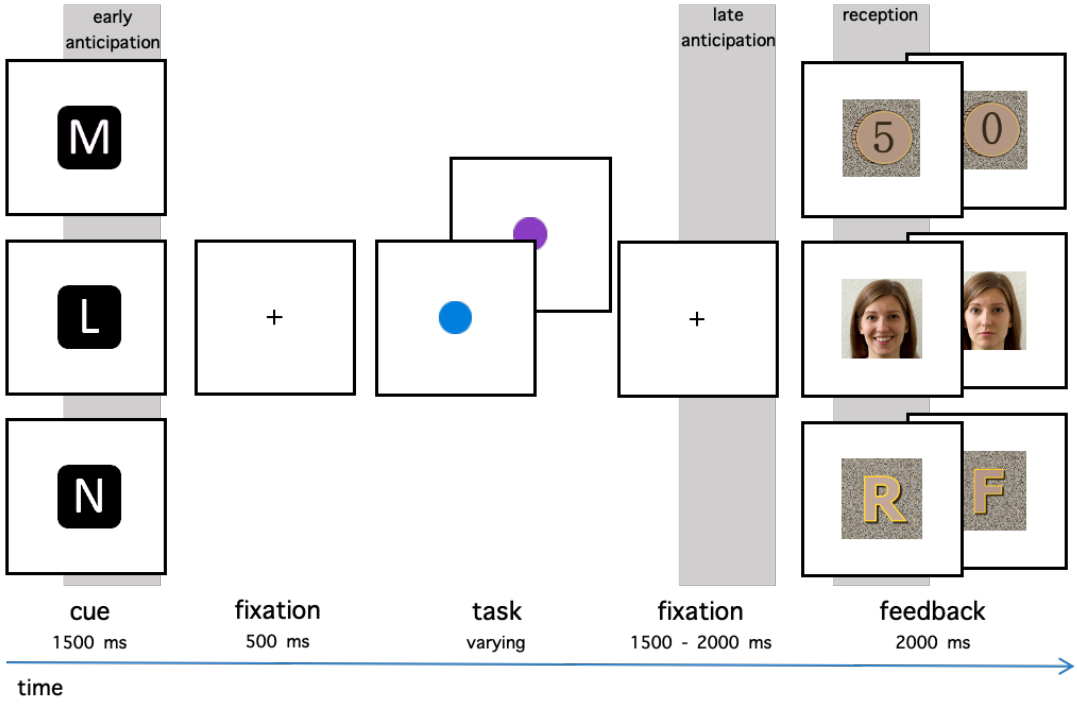

Figure 3-5 Trial structure. The possible reward in a trial was signalled with an incentive cue: M for monetary (German: Münze), L for social (German: Lächeln) and N for neutral (no reward; German: neutral). In the task, participants were asked to respond as fast as possible to a blue or a purple target with corresponding keys. In successful trials, feedback with 5-cent coin, a smiling face, or a letter "R" (correct; German: richtig), was presented in monetary, social, and neutral condition, respectively. Incorrect trials were indicated with 0-cent coin, neutral face, or a letter "F" (incorrect, German: falsch). The shaded rectangles mark approximate time windows for ERPs in early and late anticipation, and reward reception.

Each trial started with a cue presented at the centre of the screen for 1500 ms, which indicated the condition. Three conditions were introduced: social (S), monetary (M), and neutral (N). The cues consisted of white letters on black squared background (4 x 4° of visual angle). For clarity, the letters were linked to the names of potential outcomes in German: "L" for *Lächeln* (smile), "M" for *Münze* (coin), and "N" for *Neutral*. The cue was followed by a small white fixation cross (30 x 30 pixels) displayed centrally for 500 ms. Then, a blue or a purple target (a circle, 1 x 1° of visual angle) was displayed in the centre. The display time of the targets was adapting to each participant's

performance: Every four trials the display time was increased by 20% if in the last four trials no more than 1 response was correct, kept the same if 2 responses were correct, or decreased by 20% when 3 or 4 responses were correct. This procedure ensured approx. 60% accuracy on average across all participants. Upon detection of the target's colour, participants were required to press one of two response buttons as fast as possible. The colour of the target in each trial was random and the response keys corresponding to the colours were counterbalanced across participants. A trial was successful when participants pressed the correct button during the display of the target. After the button press (or the end of the display time, in case of missing responses), the pre-feedback waiting period with a fixation cross was presented for 1500 to 2000 ms (jittered across trials). Then, a feedback stimulus (matching the incentive type indicated by the cue) was presented in the centre of the screen for 2000 ms.

Correct responses in the S condition were rewarded with a picture of a happy/approving face of the main experimenter. In the M condition, a picture of a "5" coin was presented, and in the N condition, letter "R" as an indicator of successful response (for German *richtig* meaning *correct*). Incorrect responses in S, M, and N conditions were followed by a face with a neutral expression, a "0" coin, and letter "F" (for *falsch*, or *wrong*). Letters in N and coins in M were displayed on a background made of scrambled pixels of the S rewarding feedback picture (the happy/approving face). All feedback stimuli were equal in size (4 x 4° of visual angle) and luminance (ensured with the mean value of luminance in perceptual space in GIMP 2.0, which was additionally confirmed with a photometer). Participants were instructed that a "5" coin meant they were receiving additional 5 cents. The current balance was displayed after each block.

Each of the six blocks consisted of one condition. The blocks were presented pseudo-randomly: The first three blocks were presented in random order and the last three blocks repeated that order. Each block consisted of 50 trials, resulting in a total of 300 trials. Before the start of the actual experiment, three blocks (one for each condition) of 10 trials were presented as training.

3.2.2.4 Procedure and socialising

After signing the consent form, the participants were prepared for the EEG recording, which took ca. 20 min. During this time the experimenter had a light social conversation following a semi-scripted interaction. The aim was

to provide a natural acquaintance with the experimenter, with whom all participants spent the same amount of time. Moreover, this allowed the participants to familiarise with the experimenter's face in a natural fashion: from various angles and with various facial expressions. To emphasize the shared social context, the experimenter also indicated that this research was her project, and she appreciated the subjects' participation in the study. Then, participants were seated in an electrically shielded room at a distance of 70 cm from a 19-inch computer screen and 85 Hz refresh rate. To keep the light conditions constant, the room was artificially lit. Participants were asked to place their chin and forehead on a headrest in order to restrain movements. The experiment was programmed and executed in MATLAB. Task instructions were displayed on the screen and additionally repeated verbally by the experimenter. Participants were asked to identify the person on the pictures used in the S condition prior to the training and all correctly recognised the experimenter. After the recording, participants answered a number of debriefing questions on a computer screen. In the end they were debriefed and informed about in details about the purpose of the study.

3.2.2.5 Behavioural measurements

Reaction times

As a measure of performance, we collected participants' reaction times in successful trials (those which ended in positive feedback, i.e., the correct button was pressed during the display time of the target) in the task. Both shorter reaction times and higher accuracy have been previously interpreted as indexes of increased motivational and reinforcing values of the related rewards (e.g., Neuhaus et al., 2015). However, since faster responses may lead to lower accuracy, increasing response time to ensure more successful trials (and thus rewards) may be used as a strategy. Therefore, as a behavioural index of reward processing, we targeted reaction times (excluding those faster or slower than two standard deviations from a subject's mean) corrected for accuracy, i.e., the linear integrated speed-accuracy score (LISAS; Vandierendonck, 2018).

Debriefing questions

Further, we collected self-reported measures of reward responsiveness. Participants answered the following debriefing questions: *How motivated were you in the experiment?* (general motivation); *How important was the reward type to you?* (importance of condition); *How often, right after giving the response, did*

you feel you knew whether you were successful? (sense of agency), *How motivating did you find the cues?* (motivational value of cues); *How rewarding did you find the feedback pictures?* (rewarding value of feedback).

Questionnaires

Finally, we administered several questionnaires. To quantify autistic traits, we used the Autism Spectrum Quotient (AQ; Baron-Cohen, Wheelwright, Skinner, et al., 2001) and the Social Responsiveness Scale (SRS; Constantino & Gruber, 2005), which were significantly correlated in our sample, $r(65) = .66$, $p < .001$. While AQ was our primary measurement of autistic traits, we also planned to explore how the SRS relates to other measures of reward responsiveness. However, fourteen participants did not feel comfortable asking a close person to fill the SRS questionnaire for them (in contrast to the AQ which is a self-administered tool, the SRS is completed by another person). Given that the SRS scores were only available for 65 participants (7 missing in ASC, 4 in HAQ, and 3 in LAQ), we did not focus on these data any further.

To quantify further reward-related behaviour, participants were asked to fill the Behavioural Inhibition and Approach Systems Scale (BIS/BAS; Carver & White, 1994). This questionnaire assesses the behavioural activation system (BAS) responsible for increased motivation and positive affect in response to incentives, and the behavioural inhibition system (BIS), linked to experiences of anxiety, fear, and negative affect in response to threatening stimuli. BAS is further divided into three subscales: drive (inclination to pursue desired goals); fun seeking (desire for new rewards); and reward responsiveness.

Finally, to control for social anxiety traits in all statistical models, we used the Liebowitz Social Anxiety Scale self-reported (LSAS-SR; Liebowitz, 1987), which assesses anxiety related to experiencing everyday social situations.

For each questionnaire, higher scores are interpreted as higher expressions of the targeted behaviour or trait. The mean scores for each group are presented in Table 3-5.

3.2.2.6 EEG data acquisition and pre-processing

For reward reception, we quantified the P3, which is a positive potential peaking around 300 ms after stimulus onset and reflecting an elaborated cognitive and affective function linked to reward (Wu & Zhou, 2009). Based on

our previous research, we divided reward anticipation into early and late phases (Matyjek, Bayer, et al., 2020). For those, respectively, we targeted the Contingent Negativity Variation (CNV) and the Stimulus Preceding Negativity (SPN). These ERPs are slow negative waves peaking before a signal stimulus triggering a prompt action (CNV) or before receiving stimuli carrying important information, like feedback (SPN). Both CNV and SPN are linked to motivation and effort, and they reach higher amplitudes for anticipated affective or emotionally salient stimuli (Broyd et al., 2012; Brunia et al., 2012). As such, they have previously been used as indexes of reward anticipation (Matyjek, Bayer, et al., 2020; Stavropoulos & Carver, 2014b, 2014a).

The continuous EEG signal was recorded from 64 silver/silver-chloride active scalp electrodes (Biosemi Active Two) at the sampling rate of 512 Hz. An elastic cap with the extended 10-20 international electrode placement system was used. The collected signals were referenced online to the CMS-DRL ground loop, which drives the average potential as close as possible to the amplifier zero. The electrode offsets were kept within the range of $\pm 20\ \mu$V. Six external electrodes were used: four electrodes were placed at the outer canthi and below the eyes (to collect the horizontal and vertical electro-oculograms) and two were placed on the mastoids. Two online filters were applied: a 100 Hz low-pass and 0.01 Hz high-pass.

The offline pre-processing steps were performed using BrainVision Analyzer (Brain Products GmbH, Munich, Germany), in which all signals were re-referenced to average reference and filtered with a low-pass filter of 40 Hz (slope 8 dB/oct). The continuous data were segmented into segments ranging from -100 ms before to 7500 ms after the cue onset. A pre-cue baseline of 100 ms was applied. To identify and remove blinks and eye movements, an independent component analysis algorithm (restricted fast ICA) was used. Channels with low quality and noisy signals were interpolated using spherical splines of order 4 (2.7 % of all channels). Further, to exclude artifacts, a semi-automatic procedure was applied targeting signals exceeding $\pm 100\ \mu$V or voltage steps larger than 100 μV. This led to rejection of 5.39% of trials for all cue signals, 5.9% of trials for all pre-feedback, and 5.98% for all feedback signals. The data were divided into three sub-segments representing the phases: the incentive cue (early anticipation), the pre-feedback (late anticipation), and the feedback (reception). Those were ranging, respectively: from -100 ms before to 1500 ms after the cue onset; from -600 ms before feedback onset to feedback onset; and from -100 ms to 2000 ms after the feedback stimuli onset.

Across participants an average of 95 artifact-free successful trials was obtained in conditions M and S and 94 in N for the cue responses (SD_M = 5.83, SD_S = 6.08, SD_N = 8.11). In pre-feedback and feedback, the average number of successful trials was 57 (*SDpre-feedback* = 5.67, *SDfeedback* = 5.88). Average number of segments respectively for N, M, and S were in pre-feedback: 55.66 (6.37), 58.66 (4.86), and 57.19 (5.34), and in feedback: 55.46 (6.89), 58.61 (4.87), and 57.18 (5.34). The number of artifact-free segments did not vary significantly between conditions (N, M, S) in either of the phases (all $F < 1.17$, $p > .31$).

The temporal windows and regions of interest for the brain responses were chosen based on prior research and visual inspection of grand averages. For the early and late anticipation phases the time windows for the anticipatory brain responses were respectively the CNV and the SPN defined as the last 500 ms of each phase: in early anticipation this was 1000 – 1500 ms after cue onset (with -100 – 0 ms baseline), and in the jittered late anticipation phase this was -500 – 0 ms time-locked to feedback onset (with -100 – 0 ms baseline locked to the onset of the pre-feedback fixation cross). In the reception, the P3 was identified from 230 to 500 ms after feedback onset. Mean amplitudes for these time windows were calculated from electrodes Pz, P1, P2, POz, PO3, PO4, Oz, O1, O2. Finally, the mean amplitudes of the CNV, SPN, and P3 were aggregated per participant and condition and used in the statistical analyses.

3.2.2.7 Pupillary data acquisition and pre-processing

We recorded the pupil sizes in both anticipation and reception phases of reward processing. The pupil has been observed to increase in size while anticipating rewards (Cash-Padgett et al., 2018; Koelewijn et al., 2018; Schneider et al., 2018; Takarada & Nozaki, 2017). In contrast, when receiving and evaluating outcomes, the pupil is negatively correlated with their reward values (Cash-Padgett et al., 2018; Matyjek, Bayer, et al., 2021; our pre-registered expectations of dilations in this phase were yet uninformed by this recent research). The contrasting pupillary responses in reward anticipation (stronger dilation for larger rewards) and reception (stronger constriction for larger rewards) emphasise that these phases are not a unitary construct and have qualitatively different elements (Cash-Padgett et al., 2018).s

Pupillary responses were recorded binocularly with a desktop-mounted eye tracker (Eye Tribe, TheEyeTribe) with a 60 Hz sampling rate. The EyeTribe Toolbox for Matlab (https://github.com/esdalmaijer/EyeTribe-Toolbox-for-Matlab) was used to send event triggers. The calibration was conducted with

a nine-point grid and accepted when accuracy of < 0.7 degree was achieved. Data sets with poor data quality (more than 50% missing trials, with a trial removed when missing over 50% samples) were excluded from further processing and analysis (13). Offline preprocessing was performed with Matlab code published by Kret & Sjak-Shie (2018) with their default settings (upsampling was reduced from 1000 to 100 Hz). This includes blink and missing data interpolation, filtering and smoothing. Then, using a custom code in R ver. 4.0.2 (R Core Team, 2020), segmentation of the signal into phases with a subtractive 200 ms baseline correction was performed. Finally, the mean pupil size was calculated for each segment: 0 to 1500 ms after cue onset (early anticipation), -1500 to 0 ms before feedback onset (late anticipation), and 0 to 2000 ms after feedback onset (reception) and aggregated for participants and conditions.

In the remaining 66 datasets (N in LAQ, HAQ, and ASC was, respectively, 23, 24, and 19), on average 87 trials per condition in the cue signals entered analyses ($SD_M = 13.13$, $SD_N = 15.45$, $SD_S = 13.19$). In pre-feedback and feedback, average number of only successful trials for M, N, and S conditions were, respectively, 55, 53, and 53 (pre-feedback: $SD_M = 8.27$, $SD_N = 9.77$, $SD_S = 7.96$, feedback: $SD_M = 8.27$, $SD_N = 9.76$, $SD_S = 7.96$). Number of trials did not differ between conditions in the cue signals, $F(2,130) = 0.07$, $p = .936$. It did in pre-feedback, $F(2,130) = 3.13$, $p = .047$, and feedback, $F(2,130) = 3.11$, $p = .048$, but no contrasts survived corrections for multiple comparisons (all $p_{corr} >= .075$).

3.2.2.8 Data analysis

All data analyses were performed using R ver. 3.4.3 (R Core Team, 2020). The significance level for all the tests was set to .05. The data and analysis code (as well as an html file presenting all the analyses (primary and secondary) in an accessible way without the need to run the code) are available in the OSF repository: https://osf.io/vse38/.

Primary analyses

As registered, we analysed reward-related ERPs, pupil sizes, and reaction times corrected for accuracy in two approaches: 1) *population-based approach*, which includes individuals with high levels of autistic traits as compared to individuals with low levels of autistic traits (groups created based on AQ score median split); and 2) *psychopathological approach*, which includes individuals diagnosed with autism as compared to individuals with low trait levels.

Participants' responses to the debriefing questions were analysed across the three groups, with Pearson's correlation or linear models.

For reaction times, brain, and pupillary responses, we built multiple regression models with mixed effects (random intercepts for subjects) with the lmerTest package ver. 3.1-2 (Kuznetsova et al., 2017). Regression assumptions were checked and met for all models (normality, linearity, multicollinearity, homoscedasticity). Models, which violated these assumptions, were considered for outliers (based on influence and deletion diagnostics). Models with outliers were re-fitted after either overwriting a data point with the group's mean in the given condition, or exclusion of a subject's data set. Since condition is a multilevel categorical predictor (N, S, M), for the estimation of its main effect an analysis of variance (ANOVA) with Satterthwaite approximation for degrees of freedom was calculated on the models. For all reported post-hoc tests, a Holm correction was applied. Because there is no established way of calculating standardised effect sizes for mixed models' terms (Rights & Sterba, 2018), the unstandardised slope estimates can be treated as effect sizes (Pek & Flora, 2018). However, to comply to the convention, as an approximation we also calculated partial Cohen's f (f_p) from ANOVA ran on the models with the effectsize package ver. 0.3.2 (Ben-Shachar et al., 2020). As registered, we controlled for social anxiety traits by including the (centred) LSAS-SR score in all the models. Overall, all the models were built in the following form:

$$\text{DV} \sim \text{group} * \text{condition} + \text{LSAS-SR} + (1 \mid \text{subject})$$

where DV is the dependent variable (LISAS, ERP (CNV, SPN, P3), or pupil size), and the term (1 | subject) adds a random intercept for each subject. Because our hypothesis was that groups would respond similarly to different conditions (i.e., no interaction of group and condition), we first checked whether the interaction term was statistically significant. Since an insignificant effect does not mean a true negative effect, we used Bayes factors (BF) to provide an explicit quantification of evidence in favour of a model without the interaction vis-à-vis a model with the interaction (van Ravenzwaaij et al., 2019). In case of strong evidence in favour of a model without the interaction term, we continued the analysis with the model including only main effects.

Secondary analyses

Methods and results for all secondary analyses are presented in the supplementary material. As registered, we explored (1) correlations between questionnaires (AQ, BIS/BAS, and LSAS-SR), ERPs, and pupil sizes, and

(2) reaction times, ERPs, and pupillary responses also in unsuccessful (not rewarded) trials. Additionally to the registered analyses, we performed (3) dimensional analyses of AQ as a predictor of reward-related responses across all participants, and (4) exploratory analyses of the effects of age and gender in all the primary models.

3.2.3 Results

3.2.3.1 Primary analyses

The grand averages of the brain and pupil responses for all groups are shown in Figure 3-6 and Figure 3-7. Mean responses in both measures across conditions, groups, and phases are shown in Table 3-6. All analysis steps are shown in the html file (https://osf.io/vse38/) in sections 5.1.6., 5.2., and 5.3. for the population-based approach, and sections 6.1.6., 6.2., and 6.3. for the psychopathological approach.

As predicted, in none of the models (across all measures and approaches) we observed an interaction effect of group (LAQ, HAQ, ASC) and condition (S, M, N), all $F <= 2.09$, all $p >= .13$. Moreover, in all analysis we found strong evidence in favour of models without the interaction term (all $BF >= 20$; Kass & Raftery, 1995) and those models showed a better fit (based on BIC) than models including this term. Hence, in the following we report only results of models re-fitted without the interaction term. Nevertheless, all analyses steps can be found in the code and the html file.

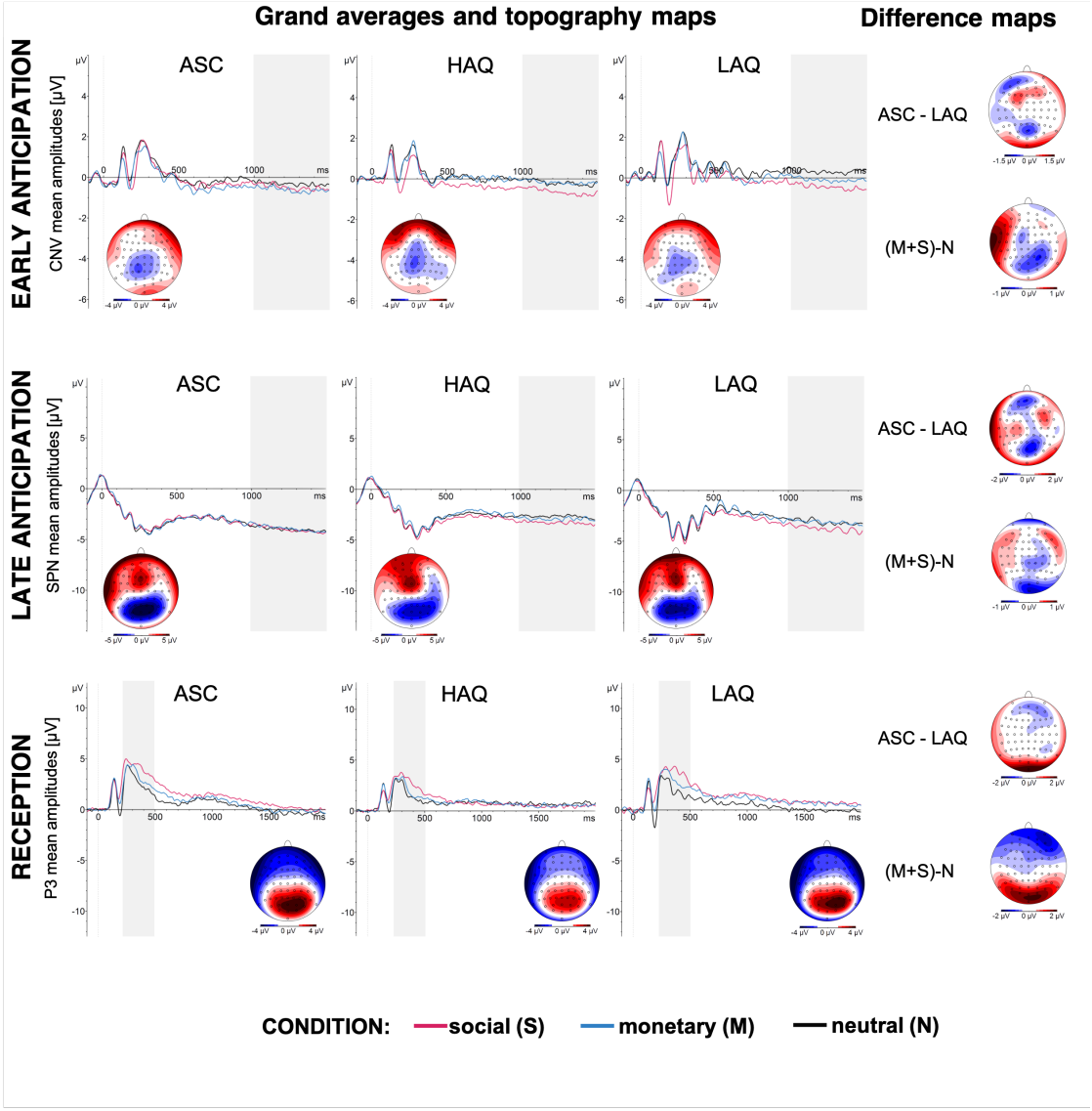

Figure 3-6 Grand averages of the ERPs. The panels show the grand averages for groups (low autistic traits, LAQ; high autistic traits, HAQ; and autism, ASC) and conditions (social, S; monetary, M; and neutral, N) for each reward processing phase: early anticipation (top panel), late anticipation (middle panel), and reception (bottom panel). The dotted vertical lines mark the onset of each phase: cue presentation in early anticipation, fixation cross in late anticipation, and feedback in reception. The grey rectangles mark the time window for analyses. Note that for the purpose of visualisation, the SPN in the late reception is plotted as aligned to the onset of the fixation cross until 1500 ms, even though the display time was jittered (1500 – 2000 ms). The analysis included the last 500 ms before the feedback in each trial.

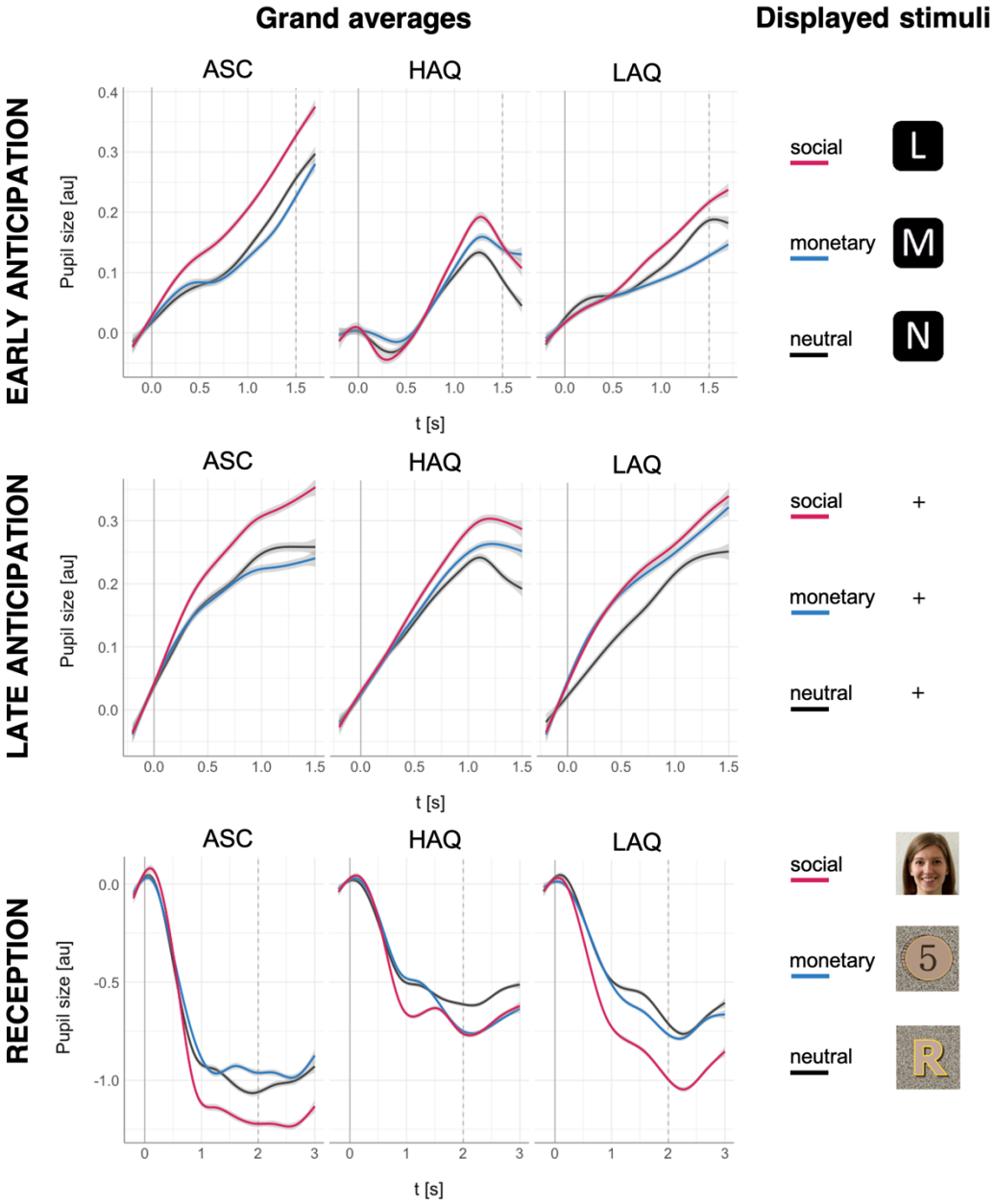

Figure 3-7 Grand averages of the pupillary responses. The panels show the grand averages for groups (low autistic traits, LAQ; high autistic traits, HAQ; and autism, ASC) and conditions (social, monetary, and neutral) for each reward processing phase: early anticipation (top panel), late anticipation (middle panel), and reception (bottom panel). On the right site are shown stimuli displayed in each phase and condition. The plots were created with generalized additive model smoothing and the grey shades show 96% confidence interval of this fit. The solid vertical lines mark the onset of each phase: cue presentation in early anticipation, fixation cross in late anticipation, and feedback in reception. The dotted vertical lines mark the end of the phase (and time window for analysis). For visualisation purposes in the early anticipation and in the reception, respectively, the following 500 ms of fixation cross and 1000 ms of the intertrial interval were plotted. Note that for the purpose of visualisation, the pupil responses in the late reception are plotted as aligned to the onset of the fixation cross until 1500 ms, even though the display time was jittered (1500 – 2000 ms). The analysis included the last 500 ms before the feedback in each trial.

Table 3-6 Means and standard deviations for ERP amplitudes, pupil responses, and reaction times in groups, conditions, and phases.

Group	Condition	Early anticipation	Late anticipation	Reception
		ERPs [μV]		
		CNV	*SPN*	*P3*
ASC	*N*	-0.32 (1.53)	-4.4 (3.42)	2.98 (1.98)
	M	-0.61 (1.77)	-4.34 (3.05)	3.33 (1.89)
	S	-0.49 (1.42)	-4.78 (3.1)	4.23 (1.94)
HAQ	*N*	-0.21 (1.39)	-2.95 (3.34)	1.73 (1.74)
	M	-0.16 (1.71)	-2.97 (3.07)	2.01 (1.83)
	S	-0.67 (1.82)	-3.52 (3.47)	2.81 (1.93)
LAQ	*N*	0.33 (1.23)	-3.3 (2.81)	2.23 (1.99)
	M	-0.1 (1.17)	-3.53 (2.45)	3.15 (2.16)
	S	-0.41 (1.13)	-3.94 (2.71)	3.82 (2.29)
		Pupil sizes [au]		
ASC	*N*	0.11 (0.15)	0.24 (0.26)	-0.78 (0.68)
	M	0.11 (0.14)	0.23 (0.25)	-0.67 (0.6)
	S	0.17 (0.19)	0.3 (0.25)	-0.78 (0.72)
HAQ	*N*	0.05 (0.29)	0.2 (0.23)	-0.38 (0.45)
	M	0.06 (0.26)	0.22 (0.31)	-0.38 (0.45)
	S	0.07 (0.38)	0.24 (0.36)	-0.45 (0.56)
LAQ	*N*	0.08 (0.21)	0.23 (0.29)	-0.37 (0.49)
	M	0.06 (0.17)	0.28 (0.27)	-0.42 (0.5)
	S	0.1 (0.29)	0.27 (0.25)	-0.54 (0.58)
		Reaction times [ms]		
ASC	*N*		291.59 (49.65)	
	M		292.79 (48.36)	
	S		296.14 (44.97)	
HAQ	*N*		290.34 (50.79)	
	M		270.16 (35.95)	
	S		289.4 (62.21)	
LAQ	*N*		292.52 (41.73)	
	M		283.48 (40.1)	
	S		290.88 (39.83)	

Population approach (low AQ vs. high AQ)

Reaction times

Condition statistically significantly predicted reaction times corrected for accuracy, i.e., LISAS scores, $F(2,100) = 11.7$, $p < .001$, $f_p = 0.48$, with fasted responses in M than N ($p_{corr} < .001$, $est = 9.99$) and M than S ($p_{corr} = .001$, $est = 7.37$). Group was not a significant predictor ($f_p = 0.13$). For details, see sections 5.1.6.

in the html file (additional analyses of uncorrected reaction times and accuracy can be found in sections 5.1.4.-5.1.5.).

ERPs

Analyses of the CNV in the early anticipation, the SPN in the late anticipation, and the P3 in the reception all yielded a main effects of condition, all $F(2,106) >= 4.61$, $p <= .012$, $f_p >= 0.3$, with the ERP responses being larger (i.e., more negative CNV and SPN, and more positive P3) for S than N (all $p_{corr} <= .012$, all $est >= .61$) and in SPN and P3 for S than M (all $p_{corr} <= .04$, all $est >= .49$). Additionally, in the reception, P3 was also statistically significantly larger for M than N ($p_{corr} = .002$, $est = 0.59$). Group was not a statistically significant predictor in these models (all $f_p <= 0.18$).

Pupil sizes

Condition was a statistically significant predictor of pupil sizes in all phases: early anticipation, $F(2,90) = 5.74$, $p = .004$, $f_p = 0.36$, late anticipation, $F(2,92) = 3.88$, $p = .024$, $f_p = 0.29$, and reception, $F(2,94) = 8.64$, $p < .001$, $f_p = 0.43$. In both anticipation phases and in reception, pairwise post-hoc tests revealed that the main effect of condition was driven by, respectively, larger dilations and larger constrictions to S than N (all $p_{corr} <= .035$, $est >= 0.04$) and in early anticipation and reception to S than M in early anticipation and reception (both $p_{corr} = .003$, $est >= 0.05$). Group did not significantly predict pupil size in any model (all $f_p <= 0.05$).

Psychopathological approach (low AQ vs. ASC)

Reaction times

The analysis of reaction times yielded a significant effect of condition, $F(2,88) = 3.64$, $p = .03$, $f_p = 0.29$, with faster responses in M than in S ($p_{corr} = .037$, $est = 5.74$). Group did not predict the responses, $f_p = 0.04$. For details, see sections 6.1.6. in the html file (and additionally 6.1.4.-6.1.5. for separate analyses of uncorrected reaction times and accuracy).

ERPs

The models yielded a main effect of condition in early anticipation, $F(2,104) = 5.25$, $p = .007$, $f_p = 0.32$, with larger CNV to S ($p_{corr} = .006$, $est = 0.45$) and M ($p_{corr} = .03$, $est = 0.36$) in comparison to N, and in reception, $F(2,104) = 20.79$, $p < .001$, $f_p = 0.63$, with the largest P3 amplitudes to S, than to M, and smallest to N (all $p_{corr} <= .004$, all $est >= 0.64$). Condition did not predict

the SPN amplitudes in late anticipation (f_p = 0.17). Group was a significant predictor only in early anticipation, $F(1,52) = 4.83$, $p = .032$, $f_p = 0.31$, where the CNV amplitudes were larger in the ASC than in the LAQ group (effect sizes for group in late anticipation and in reception were $f_p <= 0.16$).

Pupil sizes

Condition predicted pupil sizes in all phases: early anticipation, $F(2,84) = 5.57$, $p = .005$, $f_p = 0.36$, late anticipation, $F(2,82) = 5.63$, $p = .004$, $f_p = 0.37$, and reception, $F(2,84) = 8.8$, $p < .001$, $f_p = 0.46$. Pupil sizes were larger (i.e., more dilated in early and late anticipation and more constricted in reception) to S than N in all phases (all $p_{corr} <= .033$, $est >= 0.04$) and to S than M in early anticipation and reception (both $p_{corr} <= .03$, $est >= 0.05$). Group significantly predicted pupil sizes only in reception, $F(1,42) = 6.05$, $p = .018$, f_p =0.38, with larger constrictions in ASC than LAQ (in anticipation phases both $f_p <= 0.17$).

Debriefing questions

We found no significant differences in self-reported general motivation during the experiment across autistic traits, $r(79) = .05$, $p = .69$, or between groups (both $t <= 0.63$, $p >= .535$). In contrast, the condition was reportedly more important for those with less autistic traits, $r(79) = -.37$, $p < .001$, and for LAQ than ASC ($t = 3.5$, $p < .001$; in LAQ vs. HAQ, $t = -0.64$).

Three participants reported that they never or almost never knew whether they were successful in the game directly after giving response, while the rest reported they knew sometimes (16), often (24), most of the time (33), or always (3). This did not differ significantly between the groups (both $p >= .09$).

Figure 3-8 displays average ratings of motivational values of the cues and of reward values of the feedback stimuli across groups. There was a statistically significant interaction of group and condition on subjective ratings of motivational values, $F(4,152) = 2.77$, $p = .03$. Although all groups showed descriptively higher ratings for the rewarded conditions (S and M) than N, post-hoc tests revealed that this was statistically significant in the LAQ and HAQ groups (all $est >= 22.89$, $p_{corr} < .001$) but not in the ASC group (all $est >= 10.73$). Moreover, LAQ on average rated S cues higher than ASC ($est >= 23.96$, $p_{corr} = .015$).

For the analysis of subjective reward value of the feedback stimuli, we built a linear mixed model with group, condition, and outcome (successful or

unsuccessful trial) as main predictors and with their interactions. This model yielded significant interactions of group and outcome, $F(2,380) = 11.1$, $p < .001$, and of condition and outcome, $F(2,380) = 11.33$, $p < .001$. Post-hoc tests revealed that in all groups positive outcomes were rated higher than negative ones (all $est >= 46.64$, $p_{corr} < .001$), and the ratings of positive outcomes were higher in the neurotypical groups than in ASC (both $est >= 11.81$, $p_{corr} <= .008$). Feedback stimuli in all conditions were also rated higher in successful than unsuccessful trials (all $est >= 44.39$, $p_{corr} < .001$), and social and monetary rewards were rated higher than neutral positive outcomes (both $est >= 18.89$, $p_{corr} < .001$). For details and plots, see sections 4.6., 5.1.3., and 6.1.3. in the html file.

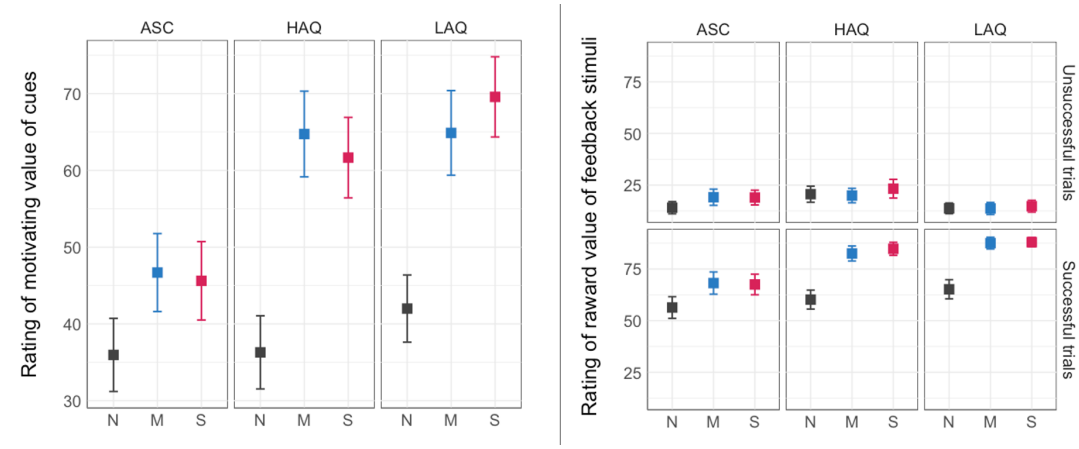

Figure 3-8 Average group ratings of (left) motivational value of the cues and (right) reward value of the feedback stimuli.

3.2.3.2 Secondary analyses

To summarise the highlights of the secondary analyses (see the supplementary material), we found that high levels of autistic traits were linked to social anxiety traits, and to stronger behavioural motivation to move away from unpleasant stimuli than to move towards desired outcomes. Further, the dimensional analyses (with AQ instead of group) paralleled the primary analyses: AQ did not interact with condition in either measure or phase, but higher AQ scores were linked to enhanced neuronal and pupillary responses respectively in early anticipation and in reception. Additional analyses revealed that the best fit for the relationship between AQ and all measures is linear, which suggests that autistic traits play a similar role in reward processing across individuals with and without autism. Finally, enhanced brain and pupillary

responses were correlated across processing phases (early and late anticipation, reception), but not with each other.

3.2.4 Discussion

In this study, we investigated responsiveness to relevant social rewards, money, and neutral outcomes across autistic traits and in autism, on multiple levels of processing. As hypothesised, using social stimuli of relevance to the participants, we found that behavioural, neuronal, and autonomic responses of individuals with autism and higher levels of autistic traits were no differently influenced by the type of outcome (relevant social reward, money, neutral outcome) than responses of those with low levels of autistic traits. However, individuals with autism, in contrast to those with low trait levels, showed enhanced reward responsiveness in early anticipation (larger CNV amplitude) and in reward reception (larger pupil constrictions). Both of these indexes have been previously linked to increased reward processing (Brunia et al., 2012; Cash-Padgett et al., 2018). These enhanced responses were also predicted by autistic traits across the whole sample in dimensional analyses. Finally, additional models revealed that the relationship between autistic traits and behavioural, neuronal, and autonomic responses is likely linear.

In line with our hypotheses, we did not observe evidence for specifically social deficits in reward processing in autism when using socially relevant stimuli. Models of all reward responses (neuronal, pupillary, and reaction times) yielded statistically insignificant interaction of group by condition and using Bayes factors, we found strong evidence in favour of no interaction being the true effect in all the models. This stands at odds with the social motivation theory, which proposes that autism is characterised by reward processing impairments (i.e., hypo-responsiveness) specifically in the social domain (Dawson et al., 2002; Dawson, Webb, & McPartland, 2005; Schultz, 2005).

A potentially critical element in our design which could explain this is the relevance of the social rewards. While a common social stimulus in reward paradigms is a picture of a smiling, unknown person (e.g., Kohls et al., 2013; Scott-Van Zeeland et al., 2010; Stavropoulos & Carver, 2014b), in this study we used photographs of the main experimenter. The experimenter's face became *familiar* to the participants during the study preparations, which they confirmed by recognising her in the photographs prior to the task. Importantly, the experimenter was also *socially relevant* in the context of the study, as she

provided explanations and instructions, engaged in a semi-scripted, casual social exchange, and was present in the laboratory throughout the course of the study, also after the completion of the task by the participants. Therefore, while many studies use faces that allow no further interaction in the study situation (even of familiar, but absent or irrelevant in the context of the task persons; Neuhaus et al., 2015; Pankert et al., 2014; Stavropoulos & Carver, 2014a), we created a relevant social context. There is accumulating evidence suggesting that faces which are more familiar and relevant elicit higher activation in the brain reward structures (e.g., Acevedo et al., 2012; Bayer et al., 2021). Moreover, familiar, but not unfamiliar faces, have been reported to elicit typical neuronal and pupillary responses in ASC (Nuske et al., 2014; Pierce et al., 2004; Pierce & Redcay, 2008). Hence, we propose that the relevance of the social stimuli used in this study is an important qualitative factor which could have normalised otherwise aberrant responsiveness (as observed in other studies using unfamiliar faces, e.g., Kohls et al., 2011; Scott-Van Zeeland et al., 2010; Stavropoulos & Carver, 2014b) to social rewards in ASC and higher autistic traits.

Further, our data provide evidence that individuals with ASC, in comparison to those with low levels of autistic traits, show enhanced reward-related processing in the early anticipation and reception of rewards (indexed by increased amplitude of the CNV and larger pupil constrictions, respectively). While these results contradict accounts suggesting reduced responsiveness in ASC to social and non-social rewards (Bottini, 2018; Clements et al., 2018; Keifer et al., 2021; Kohls et al., 2012), they are not isolated in the literature. Autism has been repeatedly linked to enhanced neuronal activation in response to various rewards (Dichter, Richey, et al., 2012; Groen et al., 2008; Pankert et al., 2014; van Dongen et al., 2015). Also, previous results from our group yielded a similar effect in early anticipation in subclinical levels of autistic traits (Matyjek, Bayer, et al., 2020).

This study investigated multiple levels of reward processing – neuronal, autonomic, and behavioural – with the aim to grasp a bigger picture of the process, which is necessary for an informed interpretation of predicted atypicalities in ASC. Across these levels, autism in our data was linked to enhanced neuronal (early anticipation) and pupillary (reception) processing of rewards, but typical performance (reaction times) and decreased ratings of the motivational and rewarding values of the stimuli. One interpretation of these results is that individuals with ASC are more sensitive to rewards on the neuronal

level (measured directly in the brain electrical activity and with pupil sizes as a proxy of the LC activity; Aston-Jones et al., 1999). The enhanced early processing in this group can be then reflecting the rapid formation of a representation of a reward and the initial anticipatory processes. However, this neuronal enhancement is weaker or absent in the later processing stages and is not translated to performance, which suggests that the motivational power of the incentive cues is not sufficient to modulate behaviour. Finally, increased autonomic measures in reward reception may indicate robust processing of the feedback (cf. with results from Baumeister et al., 2020, who observed hyperactivation of the ventral striatum during reward reception in over 200 ASC participants, although only at an uncorrected level). This, however, did not translate to a higher perceived rewarding value of the stimuli (as indicated by lower ratings of the positive feedback in ASC in our data).

Alternatively, these group differences may be an indicator of less efficient neuronal processing of rewards in ASC in the sense that larger activation is required to achieve similar performance. Importantly, the enhanced neuronal and autonomic processing was predicted by levels of autistic traits, which quantify manifestations of socio-communicative, attentional, and imaginal behaviours characteristic for ASC (Baron-Cohen, Wheelwright, Skinner, et al., 2001). This suggests that the enhanced reward responsiveness on the neuronal and autonomic levels is linked to more pronounced autistic symptomatology on the behavioural level, which cuts through the borders of diagnostic groups. This speaks to the value of the dimensional analysis of autistic traits in addition to the coarse group differences based on the diagnostic cut-off. In this vein, by exploring autistic traits as continuously distributed in the population, we showed that reward processing atypicalities are likely linked to these traits in a linear manner: the higher the autistic traits, the larger the reward-related responses.

As expected, both brain and pupil responses were consistently larger to relevant social rewards compared to neutral outcomes and (less consistently) monetary rewards regardless of autistic traits and reward processing phases (early anticipation, late anticipation, reception). This corresponds to higher ratings of motivational and reward value of the rewards in comparison to the neutral outcomes. On the other hand, reaction times corrected for accuracy were faster in monetary trials than in social or neutral ones. Although this suggests higher motivational value of the monetary rewards on performance and of social rewards on psychophysiological measures, it has been reported

before that reward magnitudes can predict subjective motivation and arousal, but not performance (Watanabe et al., 2019). Together, the larger responses in social and monetary than in neutral trials observed on multiple processing levels suggest that our paradigm was successful in capturing reward processing.

While more research is needed before firm conclusions can be drawn, our data suggest that the neuronal, autonomic, and behavioural indexes of reward processing reflect distinctive mechanisms and together offer a broader picture of this function. In line with this, ERP and pupillary responses across conditions did not correlate with each other, but in each level (neuronal and autonomic), we observed consistent correlations between reward phases. The SPN was positively associated with the CNV (both negative ERPs) and negatively with the P3 values, which suggests that the larger the late anticipation, the larger both the early anticipation and the reception of rewards. The pupil sizes in the reception phase correlated negatively with the pupil sizes in both early and late anticipation, which suggests that the larger the anticipation (indexed as increased dilations), the larger the reception (indexed as increased constrictions). These consistencies emphasise the additive explanatory values of ERPs and pupil sizes, and emphasise the importance to investigate reward function on multiple levels.

The current study design, although based on a well-established paradigm (cued incentive delay task; Knutson et al., 2005) includes several aspects which allow us to disentangle potentially confounding factors in reward processing. Firstly, we used symbolic incentive cues which were not themselves rewarding (as could be showing a coin or a smiling face as a cue; Kohls et al., 2011). Thus, we ensured that the responses in early and late anticipation were indeed reflecting reward anticipation and not reception. Further, we included a non-rewarded condition (neutral), in which informative feedback was provided, but which did not offer any external rewards. Due to this, the observed enhanced responses to the social and non-social conditions in contrast to the neutral outcomes can be interpreted as reward processing on top of feedback processing. Finally, in all statistical models we controlled for social anxiety traits, as it is linked to deficient reward processing (Richey et al., 2014), and correlates with autistic traits (see point 1.1. in the supplementary material). This allowed us to interpret the obtained results as more autism-specific.

At the same time, several limitations in this study should be noted. First, we focused on adults but reward processing atypicalities linked to autism have been shown primarily in childhood (Kohls et al., 2011; Scott-Van Zeeland et al., 2010; Stavropoulos & Carver, 2014b) and are possibly dynamic throughout development (Keifer et al., 2021). In additional explorative analyses we observed that age was linked to diminished ERP responses in late anticipation and reception (see Figure 3-14 in the supplementary material). Similarly, exploratory models yielded that females exhibited increased pupil responses in late anticipation (dilations) and reception (constrictions) than males (see Figure 3-15 in the supplementary material). However, it should be noted that groups in this study did not differ in age or gender distribution. Further, for the dimensional analyses we used the full AQ scores, but the social subscale of the AQ or the SRS would provide a more direct test of the social motivation theory's predictions. This was not possible in our data, because many participants with ASC were not comfortable with the SRS and several provided a pre-existing full AQ score (from which we could not calculate the subscales' scores). Finally, due to the need to maintain high experimental control over luminance and onset timing of the stimuli (for pupillometry and ERPs), we used static stimuli. Nevertheless, such stimuli lack ecological validity, especially in the social domain (Dziobek, 2012). Thus, future studies should attempt to replicate our results with dynamic stimuli.

To summarise, the present study provides evidence that autistic traits and autism are linked to atypical reward processing. However, in contrast to the social motivation theory, we observed enhanced neuronal and autonomic responses to both social and non-social rewards in individuals with autism in contrast to neurotypical individuals with low levels of autistic traits. Importantly, we used social stimuli of relevance to the participants, which might have increased the reward value in the social condition and potentially normalised otherwise aberrant responsiveness to social rewards in autism and higher autistic traits. By investigating neuronal, autonomic, and behavioural responses, we provided a bigger picture of reward processing, which suggests a complex mechanism manifesting differently on each level. Autism in our data was linked to enhanced neuronal and autonomic processing, typical behavioural performance, and diminished self-rated responsiveness to rewards. We suggest that to understand reward responsiveness in autism, atypicalities found on the neuronal or autonomic levels must be interpretated in relation to the behavioural manifestations of social impairments.

3.2.5 Supplementary material

All steps of the following analyses can be found in the html file available in the corresponding repository (https://osf.io/vse38/).

3.2.5.1 Questionnaires and brain-behaviour correlations

Correlations between the questionnaires, ERPs, and pupil responses were calculated using Pearson's rank correlation coefficients.

Questionnaires

We explored correlations between the AQ and other questionnaires and found statistically significant correlations for LSAS-SR, $r(79) = .67$, $p < .001$, BIS scale, $r(79) = .45$, $p < .001$, BAS drive scale, $r(79) = -.23$, $p = .041$, BAS fun seeking scale, $r(79) = -.49$, $p < .001$, and BAS reward responsiveness, $r(79) = -.31$, $p = .006$. For details and plots, see section 4.5. in the html file. Altogether, these results suggest that higher autistic traits are related to decreased social ability, increased social anxiety, higher sensitivity of the inhibition system, and reduced activation of the approach system. Thus, these data support that individuals with high autistic traits have stronger behavioural motivation to move away from unpleasant stimuli than to move towards desired outcomes.

Correlations of the brain and pupil responses

Across all successful trials, the mean SPN correlated positively with the mean CNV, $r(79) = .27$, $p = .018$, and negatively with the P3, $r(79) = -.58$, $p < .001$. This suggests that larger brain responses in late anticipation are linked to also larger responses in early anticipation and in reception.

The mean pupil sizes were negatively correlated in reception and in both early and late anticipation, $r(66) = -.52$, $p < .001$ and $r(66) = -.64$, $p < .001$, respectively. This suggests that larger pupil responses in anticipation phases (i.e., more dilation) are related to larger pupil responses in reception (i.e., more constriction).

We found no significant correlations between ERPs and pupil sizes. Figure 3-9 shows correlogram of brain and pupillary responses. For details, see section 7.4. in the html file.

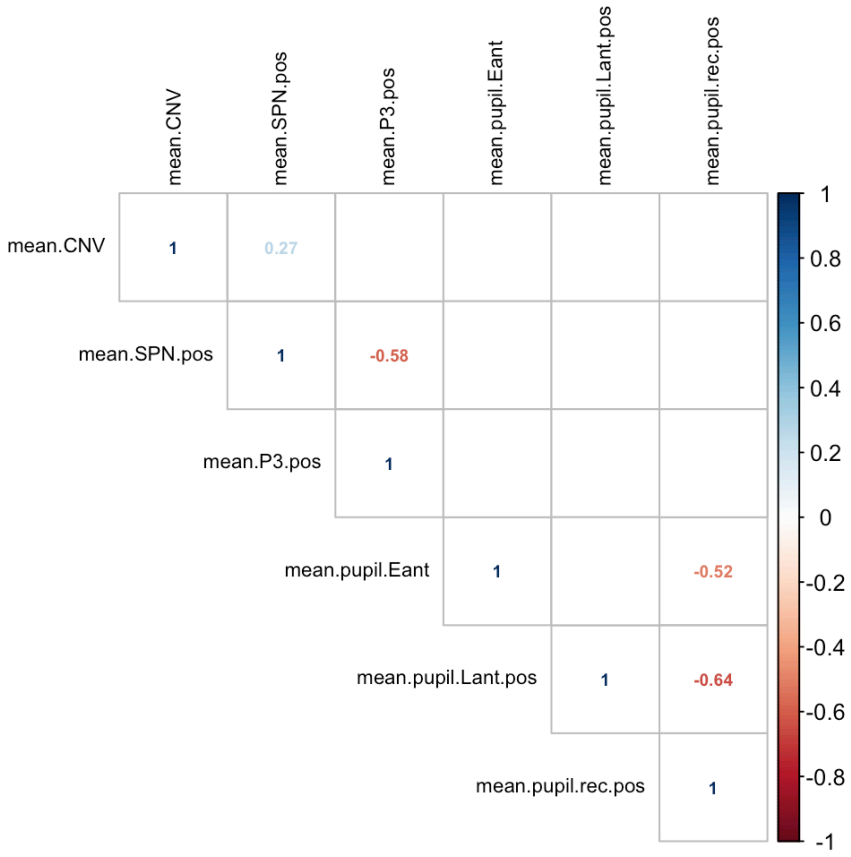

Figure 3-9 Correlogram: ERPs and pupil sizes in successful trials across conditions. Coefficients are displayed only for statistically significant correlations.

Correlations of brain, pupil, and self-reported data

The mean anticipatory brain responses (but not the P3) across conditions were found to correlate with the debriefing questions and questionnaires: Higher self-reported general motivation in the experiment was linked to larger CNV amplitudes, $r(79) = -0.26$, $p = .019$, higher BIS scores were linked to larger SPN amplitudes (in successful and unsuccessful trials, both $r(79) >= -0.37$, $p <= .005$), and higher BAS fun seeking scores in unsuccessful trials were linked to smaller SPN amplitudes, $r(79) = 0.27$, $p = .017$.

The mean pupil size across conditions correlated with self-reported importance of condition, so that the more important the condition, the weaker the pupil response in early anticipation and in reception of unsuccessful feedback (smaller pupil size in early anticipation, i.e., weaker dilations, and larger pupil size in reception, i.e., weaker constrictions), respectively $r(66) = -0.25$, $p = .04$ and $r(66) = 0.31$, $p = .012$. For details, see section 7.3. in the html file.

3.2.5.2 Effects of group, condition, and outcome (successful and unsuccessful trials) on ERP and pupillary responses in the reception phase

To explore differences between reception of successful and unsuccessful outcomes on the neuronal and pupillary responses, we built models including group, condition, outcome (successful and unsuccessful), and their interactions. The predicted P3 and pupillary responses in successful and unsuccessful trials across all groups are shown in Figure 3-10 and Figure 3-11. Full analyses can be found in section 7.2. of the html file.

For both pupillary and neuronal responses, we observed an interaction of group and outcome (both $F >= 3.53$, $p <= .03$, $f_p >= 0.13$). For the neuronal responses, this was driven by larger P3 amplitudes in ASC as compared to HAQ, for both successful and unsuccessful trials (both $p_{corr} <= .034$). For the pupil sizes, the interaction was driven by the ASC group showing significantly larger pupil constrictions to outcomes in successful than in unsuccessful trials, $p_{corr} < .001$ (no other contrasts were significant).

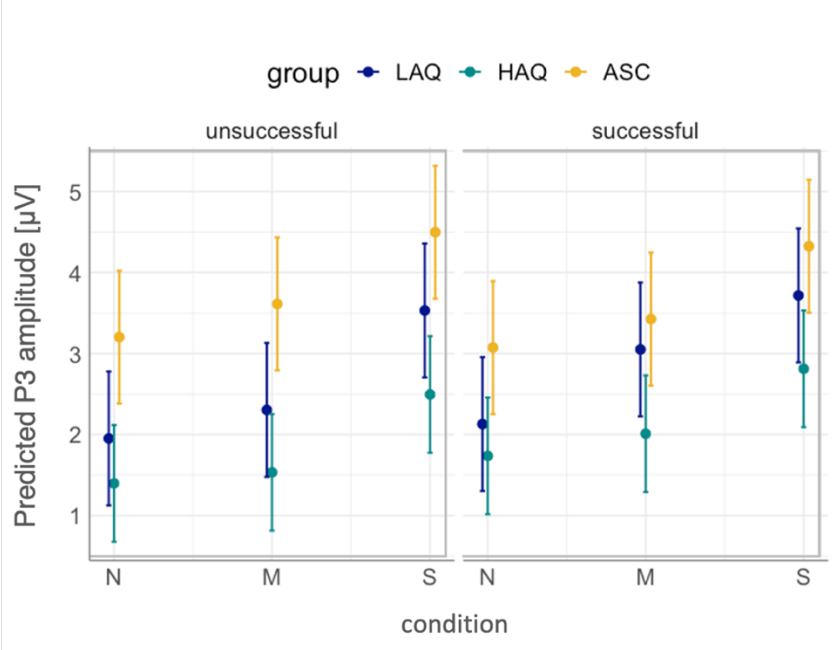

Figure 3-10 Average P3 responses in successful and unsuccessful trials across groups.

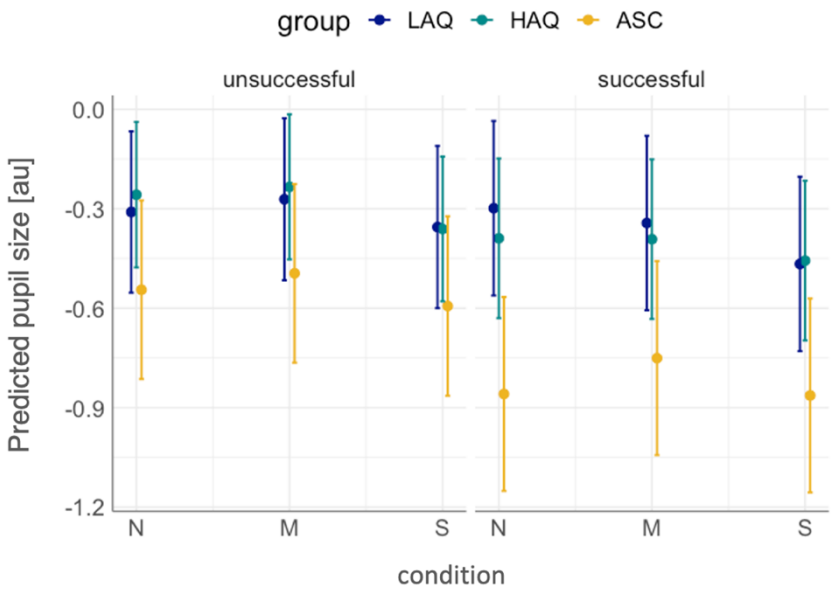

Figure 3-11 Average pupil sizes in successful and unsuccessful trials across groups

3.2.5.3 Dimensional analyses – AQ as a predictor of reaction times, ERPs, and pupillary responses

In addition to the pre-registered analyses, we explored the effects of autistic traits across the sample on reward responses (a dimension analysis). Because in the spectrum view of autism the distribution of autistic traits in the general population is continuous, we conducted exploratory analyses in which the main predictor of reward responsiveness is continuous AQ instead of group. Finally, it is conceptually interesting to consider whether the potential atypicalities in reward processing would increase linearly with higher autistic traits in the population, or whether this increase would become steeper with particularly high trait levels (for example, around the approximate cut-off of autism diagnosis). To investigate this, we also built exploratory generalised additive mixed models (GAMMs) with package mgcv ver. 1.8-31 (Wood, 2011) in the following form:

DV ~ condition + s(AQ, by = condition) + LSAS-SR + s(subject, bs='re'),

where DV is the dependent variable, s(AQ, by = condition) is a smooth term for AQ fitted separately for each condition, and s(subject, bs='re') is the random smooth for subjects. AQ and LSAS-SR were centred before they entered the statistical models. Here, we report only the main effects of those additional models and the complete analyses can be found in the analysis code

in the referred repository. Figure 3-12 shows predicted neuronal and pupillary responses across levels of autistic traits in all phases. All analysis steps are shown in section 7.1. of the html file.

ERPs

Condition was a significant predictor of the brain responses in all linear models with continuous AQ (instead of group): early anticipation, $F(2,158) = 7.76$, $p = .001$, $f_p = 0.31$, late anticipation, $F(2,156) = 3.57$, $p = .031$, $f_p = 0.21$, and reception, $F(2,158) = 4.32$, $p = .015$, $f_p = 0.23$. In all models, responses to S were larger than to N (all $p_{corr} <= .031$, $est >= 0.46$). Additionally, in late anticipation and reception, S elicited larger ERP amplitudes than M (both $p_{corr} <= .035$, $est >= 0.47$), and in reception M was linked to larger P3 than N ($p_{corr} =.002$, $est = 0.51$). The AQ score significantly predicted the brain responses only in the early anticipation, $F(1,79) = 4.28$, $p = .042$, $f_p = 0.23$ (in late anticipation and reception $f_p = 0.05$), with higher AQ scores linked to larger (more negative) CNV response.

GAMMs with continuous AQ score yielded similar pattern of effects: condition (entered as a parametrical term) significantly predicted ERP amplitudes in all models (all $F >= 4.26$, $p <= .012$) with larger responses to S than N. In the early anticipation model (and not late anticipation and reception), the AQ smooth was significant ($F = 4.12$, $p = .044$). Importantly, in all models AQ was fitted with effective degrees of freedom (edfs) of 1 (in reception edf = 1.2), which suggests that the best approximation of the relationship between autistic traits and reward-related brain responses is linear.

Pupil sizes

In all phases, the pupil sizes were predicted significantly by condition: early anticipation, $F(2,128) = 9.66$, $p < .001$, $f_p >= 0.39$, late anticipation, $F(2,128) = 5.66$, $p = .004$, $f_p = 0.29$, and reception, $F(2,132) = 5.43$, $p = .005$, $f_p = 0.4$). Responses were larger in S than in N (all $p_{corr} <= .018$, $est >= 0.04$) and in early anticipation and reception also in S than M (both $p_{corr} <= .007$, $est >= 0.05$). AQ significantly predicted pupil sizes only in reception, $F(2,128) = 5.66$, $p = .004$, $f_p = 0.33$ (in anticipation phases both $f_p <= 0.29$).

GLMMs yielded a main effect of condition in all phases (all $F >= 5.35$, $p <= .006$) with larger responses (more dilation in anticipation phases and more constriction in reception) to S than N. In all phases, the models fit better without separate AQ smooths for conditions and with edf = 1. AQ was

statistically significant only in reception with higher AQ scores linked to smaller pupil sizes ($F = 22.48$, $p = .013$).

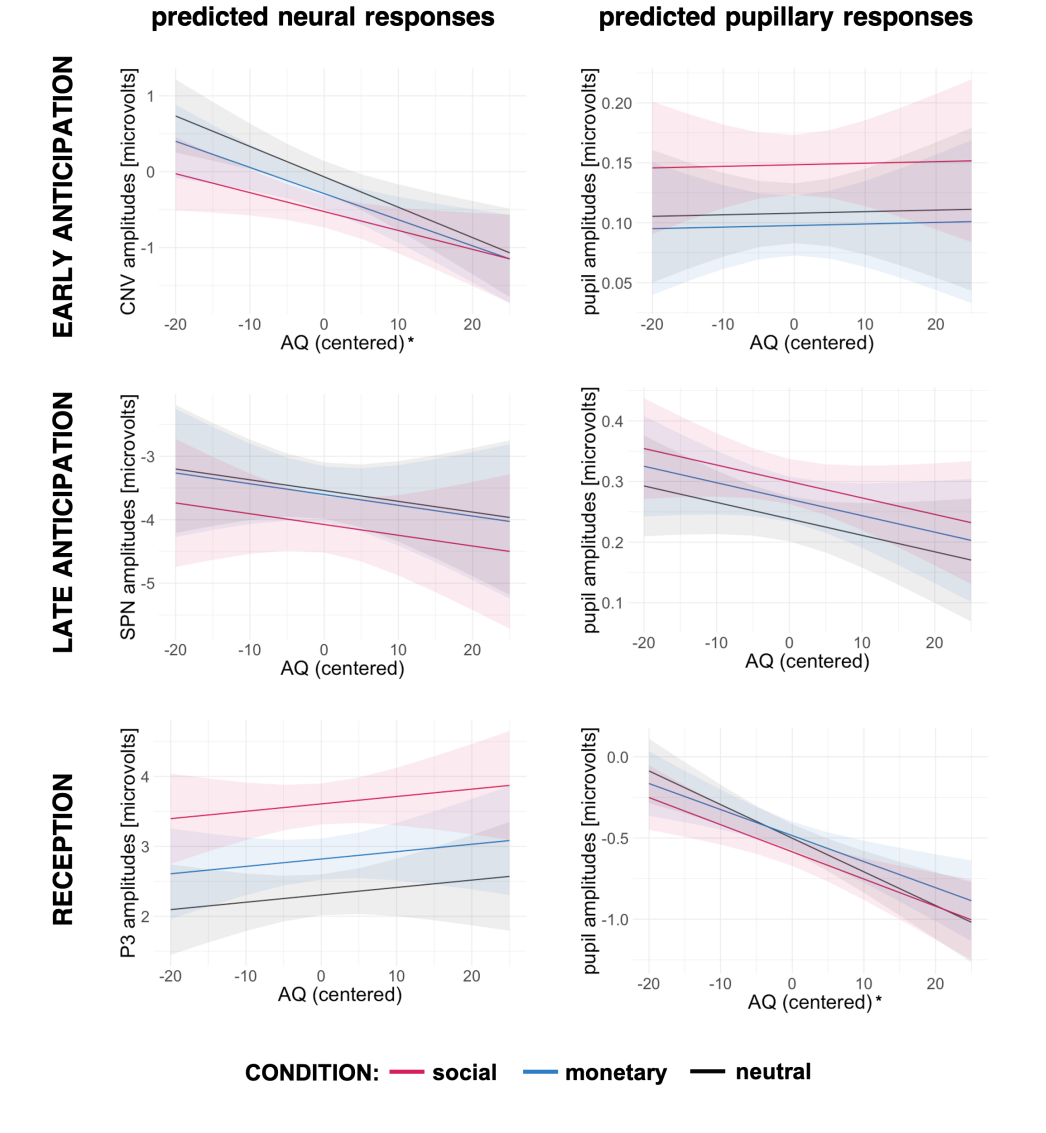

Figure 3-12 Predicted values of neuronal and pupillary responses to social, monetary, and neutral outcomes in successful trials across autistic traits (AQ) in all participants. Shadowed areas represent 95% confidence intervals. Statistically significant effects of AQ were marked with * for p < .05

Reaction times corrected for accuracy

Condition was a significant predictor of the LISAS scores, $F(2,136) = 8.6$, $p < .001$, $f_p = 0.36$, with faster responses to M than to S and N (both $p_{corr} <= .001$, $est >= 6.31$). The AQ did not significantly predict LISAS ($f_p = 0.04$). Figure 3-13 shows predicted LISAS scores across AQ.

The GAMM model showed a slightly better fit for a separate smooth for AQ in each condition, with edf = 1 for N and M and 1.3 for S. However, none of the smooths were significant. Condition as a parametric term significantly predicted LISAS ($F = 8.62$, $p < .001$), with the fastest responses in M.

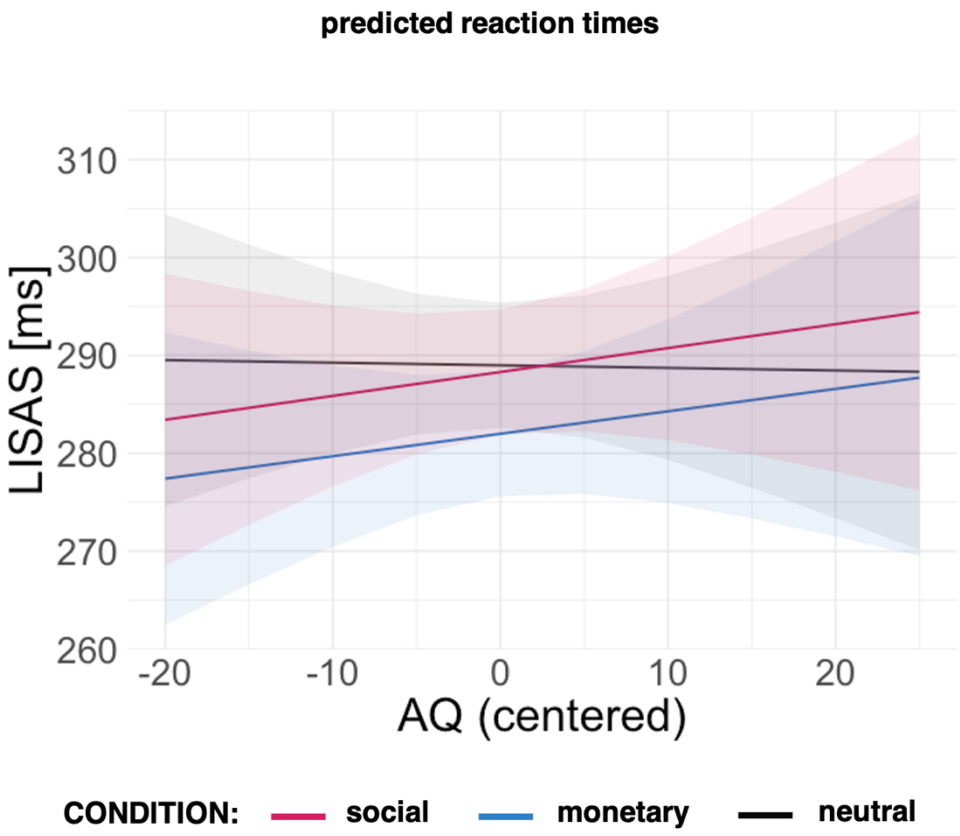

Figure 3-13 Predicted reaction times corrected for accuracy in social, monetary, and neutral conditions in successful trials across autistic traits (AQ) in all participants. Shadowed areas represent 95% confidence intervals.

3.2.5.4 Age and gender effects in ERP and pupillary models

For all primary models, we additionally explored the effects of age and gender. New models were in the form:

DV ~ group * age + group * gender + condition + LSAS-SR + (1 | subject).

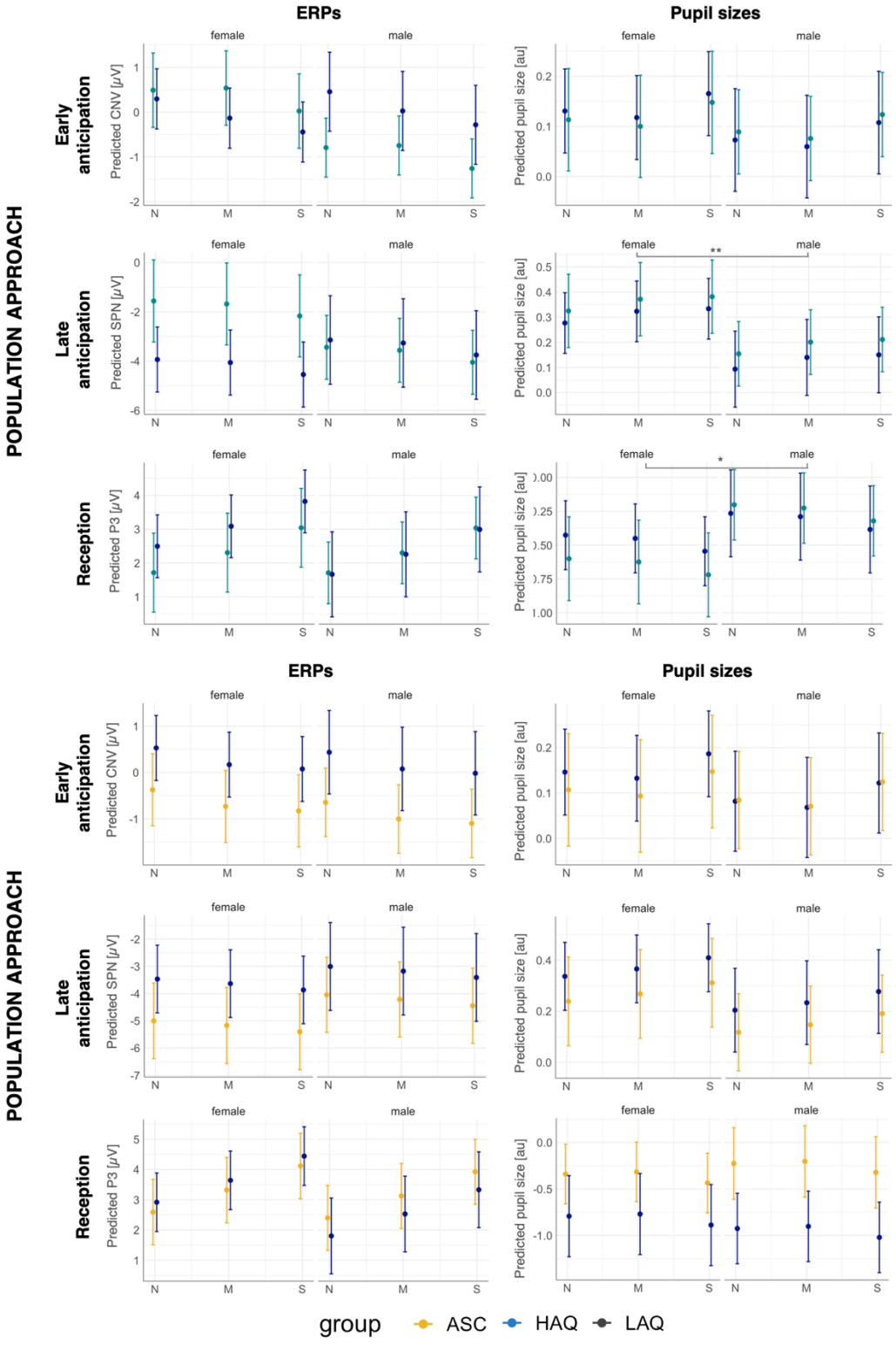

Figure 3-14 Effects of age on ERP and pupillary responses across groups (LAQ, HAQ, ASC), conditions (N = neutral, M = monetary, S = social), and phases (early/late anticipation, reception). Statistically significant predictors are marked with * for p<.05, ** for p<.01, and *** for p<.001. Details and full analyses can be found in the html file in sections 5.2-5.3 and 6.2-6.3.

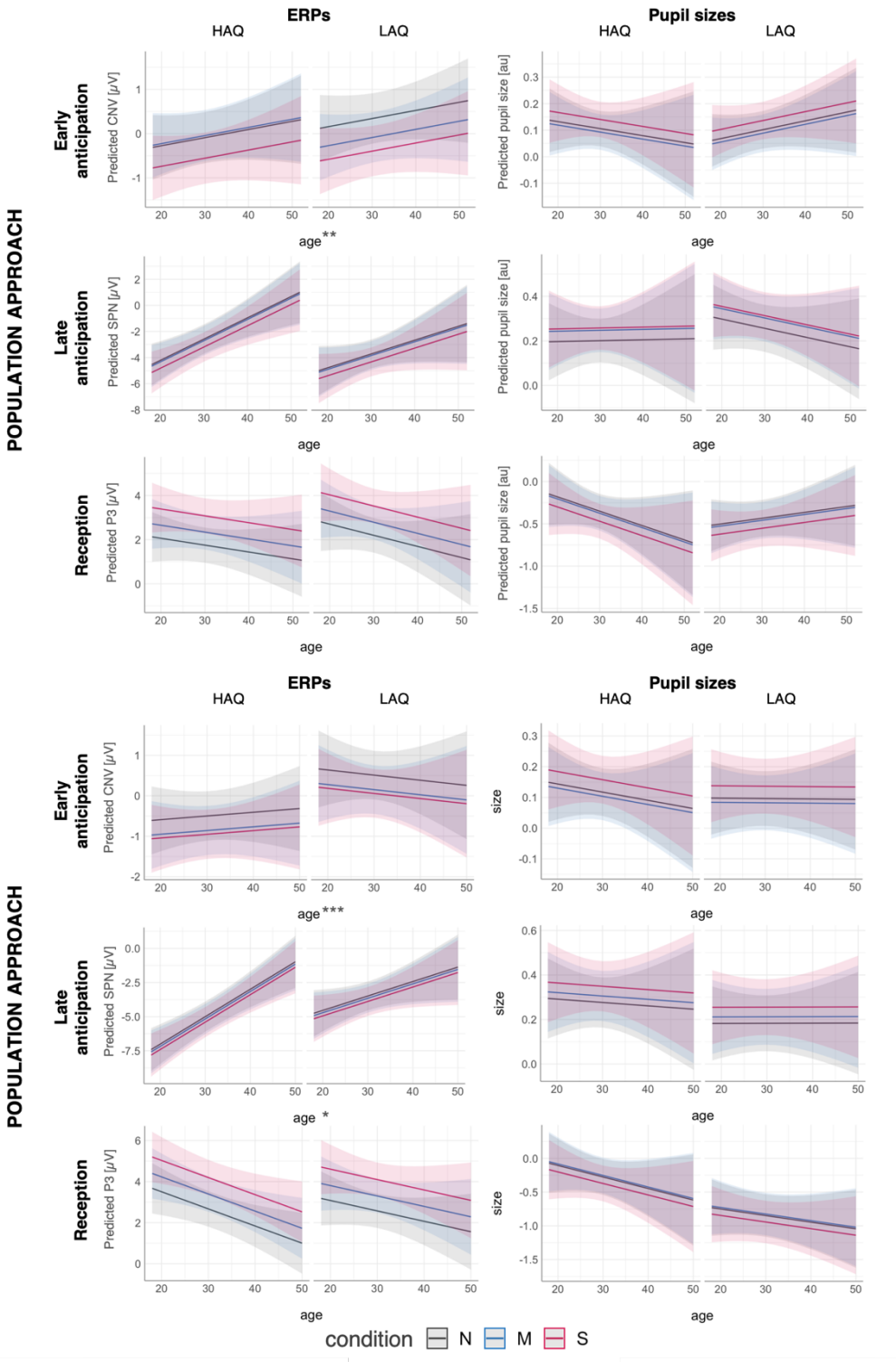

Figure 3-15 Effects of gender on ERP and pupillary responses across groups (LAQ, HAQ, ASC), conditions (N = neutral, M = monetary, S = social), and phases (early/late anticipation, reception). Statistically significant predictors are marked with * for p<.05, ** for p<.01, and *** for p<.001. Details and full analyses can be found in the html file in sections 5.2-5.3 and 6.2-6.3.

3.3 Study 3: Familiarity and rewarding context

Pupillary Responses to Faces are Modulated by Familiarity and Rewarding Context

Magdalena Matyjek, Mareike Bayer, & Isabel Dziobek

Abstract Observing familiar (known, recognisable) and socially relevant (personally important) faces elicits activation in the brain's reward circuit. Although smiling faces are often used as social rewards in research, it is firstly unclear whether familiarity and social relevance modulate the processing of faces differently, and secondly whether this processing depends on the feedback context, i.e., if it is different when smiles are delivered depending on performance or in the absence of any action (passive viewing). In this preregistered study, we compared pupillary responses to smiling faces differing in subjective familiarity and social relevance. They were displayed in a passive viewing task and in an active task (a speeded visual short-term memory task). The pupils were affected only in the active task and only by subjective familiarity. Contrary to expectations, smaller dilations were observed in response to more familiar faces. Behavioural ratings supported the superior rewarding context of the active task, with higher reward ratings for the game than the passive task. This study offers two major insights. Firstly, familiarity plays a role in the processing of social rewards, as known and unknown faces influence the autonomic responses differently. Secondly, the feedback context is crucial in reward research as positive stimuli are rewarding when they are dependent on performance.

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3.3.1 Introduction

3.3.1.1 Privileged Processing of Familiar Faces in Humans

Familiarity of faces is an important factor in the socio-cognitive functioning of humans. Immediate access to information about familiar others is crucial for successful social interactions (Gobbini & Haxby, 2007). Indeed, numerous studies have shown evidence of preferential processing of familiar faces. The familiarity of a face dramatically facilitates its recognition (Dobs et

al., 2019; Natu & O'Toole, 2011), enhances the cueing effects of the eyes (Deaner et al., 2007), and also requires less attentional resources and no conscious awareness (Gobbini et al., 2013). Social cues conveyed by familiar faces are processed and recognised faster than cues from unfamiliar faces (Visconti di Oleggio Castello et al., 2014), and on the emotional level, familiarity facilitates one's empathy towards the other (Preston & de Waal, 2002). Taken together, it seems that familiarity plays an exceptional role in human socio-cognitive functioning, which is furthered by research on social impairments, such as autism spectrum conditions (ASC). Abnormal patterns of neural activation have been reported in this population in response to unfamiliar faces (for a review, see Nomi & Uddin, 2015). These include both hypoactivation of individual cortical areas such as the fusiform gyrus, the amygdala, and the superior sulcus, and the atypicalities of distributed cortical and subcortical brain networks. However, there is evidence for typical patterns of neural activation (mainly in the fusiform gyrus and the amygdala) for familiar faces in this group (Pierce et al., 2004; Pierce & Redcay, 2008). This suggests that familiarity may normalise otherwise aberrant neural responses to faces in individuals with ASC. Altogether, familiarity has a unique standing in the human social functioning, which has even led to a shift in the proposition of humans being face experts, to that of humans being familiar face experts (Young & Burton, 2018).

3.3.1.2 Familiarity and Social Relevance of Faces

Although it is clear that the faces of familiar persons are processed differently than faces of strangers, it is important to note that there are different types of familiar faces we encounter in life: relatives, friends, colleagues, celebrities, etc. (Ramon & Gobbini, 2018). Among the qualitative differences between these categories, social relevance is the most notable. Close relatives and loved ones are more socially relevant than co-workers, and a superior is more socially relevant than an acquaintance from the gym. For the purpose of operationalising the key terms in this article, we propose the following definitions: Familiar persons are those that one recognises and has some knowledge about, but who are not necessarily personally important for the person (e.g., actors, a frequently seen salesperson in a grocery store); Socially relevant persons are those connected to one on a personal level, sharing a social context of special subjective meaning, and bearing personal importance (in the literature, social relevance is also referred to in a broader framework as 'personal

relevance', Bayer et al., 2021; or 'personal importance', Caharel et al., 2005), e.g., friends, relatives, school teachers. Both familiarity and social relevance describe spectra rather than binary categories as faces can be more (or less) familiar and more (or less) socially relevant. Moreover, socially relevant faces are often linked to affective knowledge and emotional responses of varying intensity, ranging from love for relatives and partners to feelings of acceptance or belonging in a new group context.

Following these definitions, all socially relevant faces are necessarily familiar, but not all familiar faces are socially relevant. Importantly, relevance is not merely a feature of higher levels of familiarity. For example, the face of a news presenter may be very familiar but may still not bear any social relevance due to a lack of personal importance to the person. These features can be processed detachedly, which is supported by studies with patients suffering from Capgras delusion, who believe that their loved ones are in fact imposters. Such patients can typically recognise a familiar face, but they show no autonomic response (skin conductance response) that is typically observed when seeing loved individuals (Sugiura, 2014, p. 20). Thus, the recognition process (crucial for familiarity) and the autonomic nervous system response (linked to highly socially relevant individuals) are independent to a degree. However, few studies have compared the impact of familiarity and social relevance on the processing of faces. In one such study, the N170 component was shown to be increased for personally important faces (i.e., those of a participant's mother and their own) in contrast to less familiar (celebrities) or unknown faces (Caharel et al., 2005). In another study, familiarity (friend and romantic partner vs. stranger) influenced neural processing earlier than love, i.e., high personal relevance (romantic partner vs. friend and stranger; Bayer et al., 2021). It is important to note that the definitions of familiarity and social relevance vary between studies and operationalisation of those terms is crucial for between-study comparisons.

3.3.1.3 Social Relevance and Reward Circuitry

Importantly, a number of neuroimaging studies have reported that faces of beloved individuals (i.e., familiar and socially relevant persons for whom one has strong positive emotional feelings) elicit stronger responses of the reward circuitry (among others the ventral tegmental area, striatum, anterior and posterior cingulate) than faces of less familiar persons (Acevedo et al., 2012; Aron et al., 2005; Bartels & Zeki, 2004; Bayer et al., 2021; Ortigue et al.,

2007). Thus, observing emotionally associated and socially relevant faces is more rewarding than observing faces of less familiar and relevant individuals or strangers. However, in reward research, where smiling faces are often used as social rewards, most studies use faces of individuals unknown to participants (not familiar and not relevant). This is surprising in light of the neuroimaging studies showing that the reward circuit is uniquely activated by highly relevant faces (Sugiura, 2014). Hence, it is important to empirically address whether increasing levels of familiarity and/or social relevance are linked to other reward responses than the neural responses, including behavioural self-reported reward values and psychophysiological indexes.

3.3.1.4 Reward as Property of a Pleasant Stimulus vs. as Outcome Contingent on Behaviour

It is important to note that the reward magnitude of a positive social stimulus is substantially different when its presence is contingent on one's behaviour in contrast to when it is passively viewed regardless of one's behaviour. For example, a mother's smile in response to a child's appropriate social behaviour differs from a smiling face in a commercial viewed on a television screen (for a discussion, see Matyjek, Meliss, et al., 2020). A reward value is not merely a property of a stimulus, but also lies in the receiver's subjective judgement of the stimulus (Berridge & Kringelbach, 2008). However, little research has explored the effect of familiarity (and social relevance) on the rewarding and motivating value of faces serving as feedback contingent on behaviour. Two studies investigated reward responsiveness to familiar and unfamiliar faces in children with and without ASC and found effects of the condition (Pankert et al., 2014; Stavropoulos & Carver, 2014a). One explanation for this surprising result in light of the known preferential processing of familiar faces in ASC (Pierce & Redcay, 2008) might lie in the lack of contextual importance of the faces in the study. It is possible that for autistic individuals, the reward value of the faces serving as feedback for recent actions depends on the believability that this person offers such feedback in the given situation. Thus, it is not the smiling relevant face per se that is rewarding, but rather the smile of a relevant person responding to one's actions. An argument for such disentanglement of face processing and context-dependent social meaning in individuals with ASC is offered by an observation of simultaneous normal activation in the fusiform gyrus and reduced activity in the cingulate cortex in response to specifically familiar faces (Pierce & Redcay, 2008). The fusiform

gyrus is linked to face processing and the cingulate cortex is a part of the 'default network' responsible for mentalising and social processing. This could suggest that the interplay of familiarity/social relevance and reward is dependent on the social context.

3.3.1.5 Familiarity and Social Relevance in Active and Passive Tasks

Overall, the literature suggests that faces of familiar and socially relevant persons trigger activation in the brain structures devoted to the processing of rewards. However, more research is needed to learn whether their rewarding value (1) increases with the faces' increasing familiarity and/or social relevance and (2) depends on behaviour contingency (i.e., that one has to work towards getting them or just view them passively).

In this study, we investigated whether the reward value of smiling faces depends on a feedback context and/or familiarity and social relevance. To this end, we included two tasks, namely an active task, in which participants played a repeat-a-pattern game and received social rewards (photos of smiling faces) on successful trials only (reward contingent on behaviour); and a passive task, in which participants viewed the same smiling faces with no context of performance-feedback (non-contingent presentation of the face).

We aimed to create a set of pictures of smiling faces that would ensure a wide range of levels of familiarity and social relevance for each individual, but similar levels across all participants. For this, in the present study, participants observed smiling faces of three types: (1) strangers, who are unfamiliar and socially non-relevant persons; (2) celebrities, who are personally non-relevant persons with familiar faces; and (3) experimenters, who become familiar and, to some extent, socially relevant through the importance of the shared social context of the experiment. In order to ensure the familiarity and social relevance of the experimenters, a scripted social interaction was introduced during the course of the participants' study appointment in the lab that entailed, among others, semi-scripted conversations (for similar designs, see Hayward et al., 2018; Matyjek, Bayer, et al., 2020). To capture expected intra-individual differences in the perceived familiarity and relevance of the faces, and to reflect them in the data, participants provided subjective ratings of the depicted persons. We then used the ratings as predictors of physiological responses to these faces.

3.3.1.6 Measuring Reward Processing with Eye-Tracking Pupillometry

While most reward processing studies targeting responses to familiar vs. unfamiliar faces exploit neuroimaging methods, a worthy alternative is offered by measures of the central autonomic nervous system. Pupillary responses measured with eye tracking technology allow researchers to grasp a full picture of its responsiveness, i.e., they capture the influence of both the sympathetic and the parasympathetic branches. This includes dilations caused by excitation of the sympathetic or inhibition of the parasympathetic branches and constrictions caused by the excitation of the parasympathetic or inhibition of the sympathetic branches (Liu et al., 2017). A further advantage of this technology is its non-invasiveness, which adds to the naturalness of the social context in a laboratory setting. The pupil systematically dilates in response to mental processes, such as cognitive activity, mental effort, or increasing levels of arousal (Mathôt, 2018). Importantly, the increase in its size has been linked to goal-priming with rewards (Takarada & Nozaki, 2017), to higher magnitude of possible rewards (Koelewijn et al., 2018), and to reward anticipation (Cash-Padgett et al., 2018; Schneider et al., 2018). Similarly, pleasant (and rewarding) images of smoking-related cues trigger an increase in smokers' pupil sizes (Chae et al., 2008). Moreover, pupillary responses have previously been used to discriminate between familiar and unfamiliar faces (Nuske et al., 2014). Finally, pupil size strongly correlates with the activation of the locus coeruleus (LC; Joshi et al., 2016), which plays an important role in reward processing and motivation (Hofmeister & Sterpenich, 2015). The size of a pupil is thus a promising indicator of the subjective reward value of an observed stimulus.

3.3.1.7 Aims and Hypotheses

The aim of the current study was to investigate pupillary responses (as indicators of reward processing) to smiling faces varying in their subjective levels of familiarity and social relevance. We hypothesised that the familiarity and social relevance of smiling faces, as measured via subjective ratings, would be linked to increased pupil sizes, especially in the game. This is based on: (1) the assumption that feedback from relevant and familiar faces would be more rewarding than from unknown and irrelevant faces, and (2) previous research showing that more familiar persons are regarded as being more arousing (Dobel et al., 2008) and that changes in pupil sizes can be linked to arousal as an indicator of the motivational and rewarding features of stimuli (e.g., Koelewijn et al., 2018). We did not have a directed hypothesis as to which

factor, familiarity or social relevance, would influence the pupillary responses more. We also aimed to analyse reaction times to check whether familiarity and social relevance influence performance in the following trial, as they have previously been shown to differentiate between reward conditions in speeded tasks (Kohls et al., 2011). Again, we expected that more familiar and relevant faces would improve the subsequent performance (i.e., shorten reaction times).

We also performed two secondary analyses. First, we measured participants' autistic traits to investigate their possible modulatory effects on pupil responses to smiling faces in this study. The reward value of social stimuli such as faces is proposed to be reduced in individuals with autism (Chevallier et al., 2012), and studies that measured pupil size have indicated abnormal patterns of dilation in this population (Nuske et al., 2014; Sepeta et al., 2012). For this secondary analysis, we predicted that less familiar and less relevant faces would elicit smaller dilations in individuals with higher levels of autistic traits. The reasoning is that even though social stimuli may have lower reward value for individuals with higher levels of autistic traits (Carter Leno et al., 2016), the familiarity (and social relevance) of faces likely normalises their processing (as is the case in ASC; Pierce & Redcay, 2008).

Finally, since the attractiveness of observed faces has previously been shown to influence pupil sizes (Winston et al., 2007), we collected subjective ratings of attractiveness of the faces presented in this study and included them as a covariate (predictor of no major interest) in the analyses. We also aimed to explore the correlation between ratings of attractiveness and reward value. A positive correlation would offer support for considering attractive faces as being akin to rewards (Aharon et al., 2001).

3.3.2 Materials and methods

Methods, power analyses and hypotheses were preregistered on the 25th of November 2019 at https://osf.io/h4awf. The data and analysis code in R for the current study (as well as an html file presenting all the analyses in an accessible way without the need to run the code) are available in the OSF repository: https://osf.io/623jg/.

3.3.2.1 Sample Determination and Participants

Prior to data collection, a power analysis was performed with G*power software (Faul et al., 2007) for fixed effects in linear multiple regression, with power set to 0.8, alpha set to 0.05, two predictors (familiarity and relevance), and the total number of included predictors set to four (familiarity, relevance, attractiveness, and trial number). This analysis showed that, to observe a medium effect size of $f^2 = 0.15$, a total sample size of 68 is required. Participants were recruited via eBay (a popular online advertising service in Germany), social media, flyers distributed on the university's campus, and through participant databases of the Berlin School of Mind and Brain and Humboldt-Universität zu Berlin. All participants were between 18 and 40 years of age, had no self-reported history of psychological illness in the last six months, were proficient in English, and had normal or corrected-to-normal vision. A total of 84 volunteers participated in the study. Fourteen data sets were subsequently rejected due to poor data quality or failed attention checks (for details, see 3.3.2.6). The remaining sample of 70 participants consisted of 45 females and 25 males, with an average age of 27.77 years ($SD = 5.17$), which did not differ between the genders, $t(44.74) = -0.45$, $p = .66$. The study was approved by the Ethics Committee of the Institute of Psychology, Humboldt-Universität zu Berlin (nr 2019–24). Participants provided prior informed written consent.

3.3.2.2 Stimuli and Materials

The stimuli set consisted of pictures of 10 females: two experimenters, two strangers, and six celebrities. All experimenters and strangers consented in writing to the use of their photographs in the study. Pictures of celebrities were selected from the internet. We targeted pictures of popular actresses and singers aged between 20 to 40 years without excessive make up, with a straight gaze and smile, who were facing the camera. The pictures of experimenters and strangers (personal contacts of the researchers with no connection to the study) were taken according to these criteria. The background was removed from all photos, which were resized to 238 × 238 pixels (seven visual angles) and transformed into greyscale. Finally, their brightness and contrast were adjusted so that all matched in terms of luminance (ensured with the mean value of luminance in perceptual space in GIMP 2.0, which was additionally confirmed with a photometer). Photo editing was conducted with GIMP 2.0.

The experiment was run using a 19-inch flat-screen monitor with 1024×1280 pixel resolution and a 60 Hz refresh rate. The experiment was programmed and executed in MATLAB. Pupillary responses were recorded binocularly using a desktop-mounted eye tracker (Eye Tribe, TheEyeTribe) at a 60 Hz sampling rate and the EyeTribe Toolbox for MATLAB (https://github.com/esdalmaijer/EyeTribe-Toolbox-for-Matlab). Eye Tribe provides pupil measurements in arbitrary units (not mm or pixels). Prior to each task, the eye tracker was calibrated with a nine-point grid. Calibration was accepted when <0.7 degree of accuracy was achieved.

3.3.2.3 Procedure and Tasks

Socialising

Upon arrival, participants were fetched at the entrance of the university building by one of two experimenters (randomly assigned), who introduced herself and maintained a semi-scripted, naturally flowing social conversation on their way to the laboratory. There, the experimenter explained the study and her role in it (a master student doing a lab rotation) and encouraged questions. After acquiring signed consent, she presented the participants with all the face stimuli and asked them to indicate the faces they recognised. This was done to ensure that participants recognised their experimenter in the picture, recognised at least one celebrity (and did not exhibit any excessive positive or negative affection towards them), and were unfamiliar with at least one stranger. Based on their answers, the experimenter selected one celebrity and one stranger. This part also served as further natural socialising of the participants and the experimenter, who led a light, semi-scripted social conversation to increase their social relevance (shared context and social interaction) and familiarity through an extended exposure (approximately 10-min conversation with various expressions and viewing angles of the experimenter's face). The overall duration of the interaction between experimenters and participants prior to the tasks was approximately 20 min.

Tasks

The lab was an artificially lit room (with constant illumination for all participants) with covered windows to keep the light conditions constant. A chinrest was used to limit head movements and to maintain the distance between participants and the screen at 50 cm. All participants completed two tasks in counterbalanced order: a passive viewing task and a repeat-a-pattern

game. Prior to each, the eye tracker was calibrated. Participants were instructed to keep their eyes fixed on the centre of the screen.

In the repeat-a-pattern game modelled on the popular Simon game (Hasbro Gaming), participants were instructed to quickly repeat a pattern of appearance of four coloured dots that was presented on the screen (in terms of locations and colours), by pressing the corresponding buttons on a gamepad (both in terms of locations and colours, i.e., replicating the pattern). They were informed that they would see a smiling face as positive feedback in case of success, or a red cross in case of failure. To further their motivation in the game through an element of competition, participants could also place their nicknames and scores on the wall of best scores after completing the tasks. The game consisted of six blocks of 18 trials, resulting in a total of 108 trials (circa 8 min). In each trial, participants first saw a fixation cross for 500 ms. Then, four circles (50 pixels diameter) of red, yellow, green, or blue colour were presented with 0.1 s blank screen in between. The circles were displayed 50 pixels from the centre of the screen reflecting the topography and colours of the gamepad's buttons. To create a dynamic setting and sustain motivation to play, in the first two blocks the display time of the circles was 0.2 s, in the next two blocks 0.17 s, and in the last two blocks 0.14 s. After the pattern was shown, the word 'GO!' was displayed in the centre of the screen for 0.2 s, triggering the response. Participants then repeated the pattern on the gamepad, which was followed by a 0.5 s blank screen and feedback. In case they failed to press four buttons within 3 s or to repeat the pattern correctly, the trial was unsuccessful, in which case a red cross was presented in the centre of the screen for 0.5 s. In successful trials, a smiling face of a stranger, celebrity, or the experimenter (in a randomised order) was presented at the centre of the screen for 3 s.

In the passive viewing task, the same pictures (of the same experimenter, celebrity, and stranger as in the game) were displayed in random order for 3 s with a 500 ms inter-trial interval. As in the game, the 108 trials were divided into six blocks (circa 6 min). Additionally, to ensure that participants paid attention to the faces, a 1-back task was introduced: Eight times throughout the task (at least once in a block) one of the faces was presented in a red frame with a question 'is this the face you saw in the last trial?'; participants responded yes or no by pressing a button. Since the face had to be stored for only 0.5 s (the intertrial interval), attentional and memory demands were likely very low.

3.3.2.4 Ratings and Questionnaires

After completing both tasks, participants rated the faces used in the tasks on the dimensions of social relevance, familiarity, attractiveness, and reward value, via an online survey administered with the SoSci Survey platform, www.soscisurvey.de (Leiner, 2019). Participants answered the following questions (separately for each factor): *How socially relevant/familiar/attractive do you find the people presented in the pictures at the moment?/How rewarding did you find these pictures?* Additionally, short descriptions were provided to ensure all participants shared an understanding of the concepts in question. These were, respectively to the questions: *a socially relevant person is someone you are connected to, who is important for you for some reason, who you share a social context with*; *a familiar person is someone you know, recognise, have some knowledge about*; *an attractive person is someone you find aesthetically pleasant, pleasing, interesting, beautiful, arousing, or desirable*; *when you saw these faces as feedback in the game with the coloured buttons/the passive looking task, how rewarding were they to you?* We were aware of the fact that the reward ratings for faces in the passive viewing task were not reflecting rewards per se, as in this task the smiling faces were positive stimuli presented in the absence of any actions performed by the participants. However, to allow exploratory comparison between tasks, we asked for the reward ratings of the faces in both tasks (repeat-a-pattern game and the passive viewing). All ratings were given on a 100-point scale with extremes labelled as 'not at all' (0) and 'very' (100).

For an analysis of autistic traits' effect on arousal measurements in the tasks, participants also filled out the 10-item Autism Spectrum Quotient (AQ; Baron-Cohen, Wheelwright, Skinner, et al., 2001). Additionally, they filled out the behavioural inhibition/approach scales (BIS/BAS; Carver & White, 1994), which addresses whether individuals are motivated by pursuit of rewards (the BAS system) or avoidance of punishment (the BIS system), and the Liebowitz Social Anxiety Scale (LSAS; Liebowitz et al., 1985), which addresses anxiety linked to social stimuli and situations, e.g., social judgement.

3.3.2.5 Data Preprocessing

Pupillary Responses

Offline pre-processing of the pupillary data was performed using MATLAB, with a procedure proposed by Kret & Sjak-Shie (2018) with their default settings. Pre-processing included blink and missing data interpolation (artifacts identified as dilation speed outliers and edge artifacts, trend-line deviation outliers, and temporally isolated samples), filtering, calculating mean pupil size from both eyes, smoothing, and up-sampling to increase the temporal resolution and smoothness (for details, see Kret & Sjak-Shie, 2018). Segmentation and subtractive 200 ms baseline correction were subsequently performed in R ver. 4.0.2 (R Core Team, 2020). The mean pupil size across a time window within the segment was calculated and used in the analyses. The time window was based on visual inspection of the averaged pupillary responses (see Figure 3-16) resulting in 1–3 s for the game and 0.5–2 s for the passive task. The difference in the time windows (which were used for response averaging) results from the different overall shape of the phasic pupil responses to stimuli presentations in the repeat-a-pattern game and the passive viewing (for details, see section 3.3.3.3). Averaging of trials was performed to increase the signal-to-noise ratio of the signal.

Reaction Times in the Game

Reaction times were recorded as the last button press in an attempt to repeat the pattern in the game. Unsuccessful trials (incorrect responses or responses that took longer than 3 s) were removed from the data sets (16.44 trials on average). Three participants showed low accuracy, i.e., lower than 2 SD from the sample's mean (on average, participants were successful in 92 trials). We built models both with and without the data from these three participants and observed similar results. We therefore here describe the models generated without the exclusion of these participants, although for the sake of completeness, both models can be found in the analysis code (https://osf.io/623jg/, Section 5.1.7). Trials with reactions times longer or shorter than 2 SD from the mean of each participant and longer than 3 s were removed from the data set (4.11 trials on average).

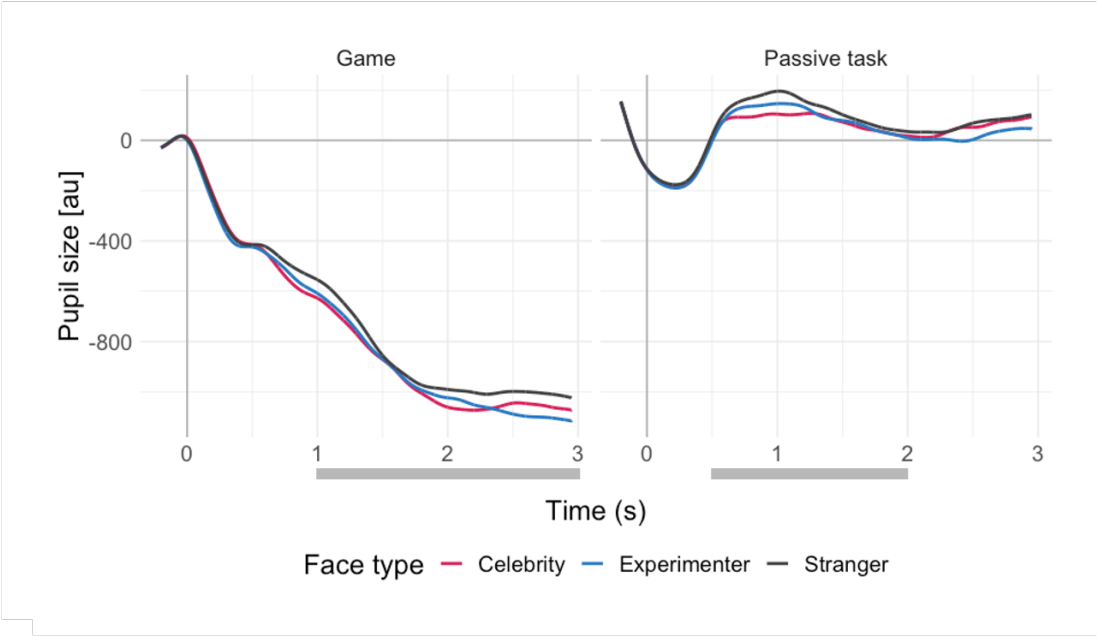

Figure 3-16 Average pupil sizes (in arbitrary units) in response to stimuli in both tasks across face types (celebrity, experimenter, stranger). The averages are aligned at time 0, which marks the onset of a stimulus presentation (the 200 ms prior to this point comprise the baseline). Grey lines mark the time window used in analyses. Note that the responses are grouped for face types for the purposes of visualisation only (the analyses were conducted with subjective ratings of familiarity and social relevance).

3.3.2.6 Data Rejection

As registered, full data sets were removed if participants failed to give the correct response in four or more trials of the 1-back task in the passive viewing task (two data sets; for details, see tasks' description above), or if the data quality of the acquired signal was insufficient. Insufficient data quality was defined as 50 or more percent of trials rejected due to missing data samples within each trial (50% or more) or more than 50% missing data samples in a trial's baseline. Missing data samples were mainly blinks and fixations away from the stimuli. Since rotating the eyeball to look at distant points from the centre of the screen causes an artificial decrease of the pupil size (Kret & Sjak-Shie, 2018), all fixations beyond the area of interest were removed. The area of interest was defined as the size of the stimuli plus two visual angles (not one as preregistered, to match the previous literature, Brisson et al., 2013).

These restrictions led to the rejection of 14 data sets. In the remaining data from 70 subjects, the number of trials across face types (experimenter, stranger, celebrity) was not significantly different in either of the two tasks, $F(2,207) = 0.009$, $p = .99$ (game) and $F(2,207) = 0$, $p = 1$ (passive task).

3.3.2.7 Data Analyses

All data analyses were performed using R ver. 4.0.2 (R Core Team, 2020). The significance level for all the tests was set to .05. The analysis of the game data only included successful trials (where faces were presented as positive feedback). For all analyses (subjective ratings, pupillary responses, reaction times), we used multiple regression analyses with mixed effects with the lmerTest package ver. 3.1-2 (Kuznetsova et al., 2017) and with treatment contrasts. Random intercepts for participants were used in all models. Additional random intercepts for stimuli (10 pictures used in the study) were used in the models, but in the game data (both pupillary responses and reaction times) variance of this term was 0, which suggests a singular model, and thus this term was eliminated from the game model. Assumptions for multiple regression were checked (normality, linearity, multicollinearity, homoscedasticity). The social relevance and attractiveness ratings models showed moderate skewness in the residual plots and were subsequently re-fitted with transformed data. The distribution of residuals in the initial reaction times model was positively skewed, which violated the normality assumption for linear models. Instead of transforming the data, which would make the estimates not readily interpretable (Speelman et al., 2015), we used a generalised linear mixed model with raw reaction times with fitted inverse Gaussian distribution and the identity link function, which also ensured that the estimates could be considered direct effect sizes. Confidence intervals for this analysis were calculated via the confint function of the R base package stats with method Wald. Marginal and conditional R^2 were calculated as measures of goodness of fit for mixed models (Nakagawa & Schielzeth, 2013), in which marginal R^2 (R^2_m) reflects variance explained by fixed factors, and conditional R^2 (R^2_c) the variance explained by the entire model. Since there is no agreement on a method for estimating standardised effect sizes for individual terms in linear mixed effect models (Rights & Sterba, 2018), we used an indirect method for their estimation: partial Cohen's *f*s (f_p) were calculated with effect size package v. 0.3.2 (Ben-Shachar et al., 2020), which calculates these from an analysis of variance run on the models. The *p*-values were computed via Wald-statistics approximation (treating *t* as Wald *z*) and corrected with package multcomp v. 1.4-13 where appropriate (Hothorn et al., 2008). *P*-values for exploratory analyses are intentionally not provided. Plots and tables of the models were created with the sjPlot package v. 2.8.4 (Lüdecke, 2020).

3.3.3 Results

3.3.3.1 Subjective Ratings—Planned Analyses

Table 3-7 shows the mean ratings (with standard deviations) and results of analysis of variance (ANOVA) performed on regression models with random intercepts for subjects and (1) one predictor: face type (stranger, experimenter, celebrity) for social relevance, familiarity, and attractiveness, or (2) two predictors: face type and task (repeat-a-pattern game, passive task) and their interaction for reward value. Once again, the analyses including reward value of faces in the passive task were included for completeness, but the meaning of reward value across the two tasks is likely different due to the presence (in the repeat-a-pattern game) or absence (in the passive viewing) of the feedback (and thus reward) context.

Table 3-7 Mean subjective ratings (and standard deviation) of social relevance, familiarity, attractiveness, and reward value for each type of face (experimenter, celebrity, stranger). *p*-values < 0.01, <0.001 are marked with **, and ***, respectively.

	Social relevance	Familiarity	Attractiveness	Reward value	
				Game	Passive
Experimenter	42.77 (30.34)	69.53 (27.84)	57.01 (23.84)	75.37 (27.03)	39.46 (38.18)
Celebrity	26.51 (31.86)	75.37 (27.03)	71.76 (23.78)	54.66 (30.68)	42.64 (28.32)
Stranger	11.16 (19.55)	39.46 (38.18)	47.91 (29.71)	44.54 (30.45)	69.53 (27.84)
ANOVA					
Face type	$F(2,140) = 47.42$ ***	$F(2,140) = 50.07$ ***	$F(2,140) = 17.76$ ***	$F(2,350) = 5.27$ **	
Task	-	-	-	$F(1,350) = 9.41$ **	
Face type x Task	-	-	-	$F(2,350) = 50.51$ ***	

Face type was a significant predictor in all models with one predictor. Post hoc analyses (with Holm correction) revealed that, in terms of social relevance, the experimenter was rated significantly higher than both the celebrity and the stranger, and the celebrity was also rated higher than the stranger (all $ps_{corr} < .001$). Both the experimenter and the celebrity were rated as more familiar than the stranger ($ps_{corr} < .001$), but similarly to each other ($ps_{corr} = .13$). On average, the celebrity was rated as being more attractive than the

experimenter and the stranger (both $ps_{corr} < .001$). Altogether, these results suggest that the experimenter and the celebrity were perceived by the participants as being more familiar and socially relevant than the stranger. The experimenter was also perceived as being more socially relevant, but not more familiar, than the celebrity.

Exploratory analysis of the reward value of faces revealed an interaction of face type and task, which is presented in Figure 3-17a. Post hoc comparisons (the complete list of adjusted *p*-values can be found in the supplementary material, Table 3-10) confirmed that in the game, the experimenter's face was perceived as more rewarding than the other two faces, whereas in the passive task the most rewarding face was that of the stranger. Moreover, while both the experimenter and the celebrity were rated as more rewarding in the game than in the passive task, it was the opposite for the stranger.

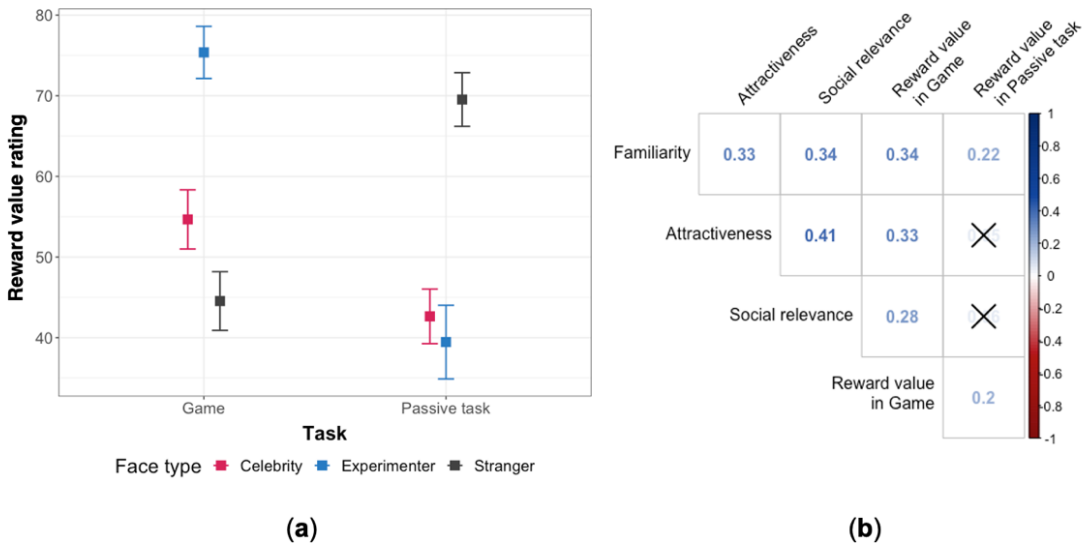

Figure 3-17 (a) Mean subjective ratings of the reward value of each type of face in the repeat-a-pattern game and the passive task. The error bars represent standard errors. **(b)** Correlogram (Pearson) of the ratings: social relevance, familiarity, reward value, and attractiveness. For clarity, the crosses mark statistically insignificant correlations (*p*-values were adjusted with Holm correction), however, this is an exploratory analysis and *p*-values should not be considered relevant.

3.3.3.2 Subjective Ratings—Exploratory Analysis

We explored correlations between the subjective ratings. We were particularly interested in the relationship between attractiveness and reward value. A correlogram with all ratings, shown in Figure 3-17b, suggests that higher

perceived attractiveness is linked to higher reward value, but only in the repeat-a-pattern game.

3.3.3.3 Pupillary Responses—Planned Analyses

The average pupil sizes in response to the stimuli (stranger, celebrity, and experimenter) in both tasks are shown in Figure 3-16. Importantly, these categories were not used as predictors in the regression models; instead, we used the subjective ratings provided by the participants. The overall shape of the pupil responses reflected the differences between the tasks. In the repeat-a-pattern game, stimuli were presented as feedback to the participants' responses, which caused large pupil dilations, reflecting the cognitive load of the task (see Figure 3-19 in the supplementary material). In turn, this caused the pupils to decrease in size during the feedback (face) presentation (return to baseline). Since in the passive viewing task there were no systematic large dilations prior to the stimulus onset, the pupil responses in this task showed less fluctuation.

For both tasks, we built multiple regression models with continuous and centred subjective ratings of social relevance and familiarity of the stimuli as main predictors. The ratings of reward value were also included in the game model, but not in the passive viewing model (as reward value in the context of passive viewing is not meaningful). We controlled for attractiveness and time effects by including attractiveness ratings and trial numbers as covariates. The models are shown in Table 3-8.

In the game, we observed a statistically significant effect of familiarity, with smaller pupil sizes for more familiar faces. The results also show the effects of trial number in both tasks such that, in the repeat-a-pattern game, the pupil sizes increased with time, while in the passive viewing task they decreased with time. In the repeat-a-pattern game, the effect sizes were: $f_p = 0.03$ for trial, $f_p = 0.03$ for familiarity, all others ≤ 0.02; in the passive task, the effect sizes were: $f_p = 0.07$ for trial, all others ≤ 0.05.

We tested gender, LSAS, and BIS/BAS scales to check whether they would improve the models' fit. As none of these aspects did, they were thus not further considered. Furthermore, we tested whether the two experimenters in the study had different effects on the pupillary responses and found no such effect (for both analyses, see points 4.1.5 and 5.1.5 in the analysis code).

Table 3-8 Mixed effects models investigating the effects of social relevance, familiarity, and reward value on pupil size in the repeat-a-pattern game and in the passive viewing task (with attractiveness and trial number as covariates).

	Passive viewing task		**Repeat-a-pattern Game**	
Estimates (95 % CI)	*Estimates*	*t-value*	*Estimates*	*t-value*
Intercept	174.00 *** (99.02 – 248.97)	4.55	-993.36 *** (-1155.60 – -831.12)	-12.00
Social relevance	-0.08 (-1.21 – 1.06)	-0.13	0.83 (-0.62 – 2.28)	1.12
Familiarity	0.43 (-0.58 – 1.45)	0.84	-1.72 * (-3.03 – -0.41)	-2.57
Attractiveness	-0.08 (-1.26 – 1.10)	-0.13	1.41 (-0.10 – 2.92)	1.83
Trial number	-2.15 *** (-2.98 – -1.32)	-5.06	0.96 * (0.02 – 1.89)	2.01
Game: Reward value			-0.71 (-1.99 – 0.57)	-1.09
Random Effects				
σ^2	756522.55		1394768.97	
τ_{00}	41903.35 $_{code}$		415711.60 $_{code}$	
	3206.80 $_{item}$			
ICC	0.06		0.23	
N	10 $_{item}$		70 $_{code}$	
	70 $_{code}$			
Observations	6211		6408	
Marginal R^2 / Conditional R^2	0.004 / 0.060		0.003 / 0.232	

* p<0.05 ** p<0.01 *** p<0.001
ICC = interclass correlation coefficient
τ_{00} = between-subject-variance

3.3.3.4 Reaction Times—Planned Analysis

Since in the repeat-a-pattern game participants did not know which face they would see after a successful repetition of a pattern in each trial (face type was randomised for all participants), we built a generalised linear mixed model predicting reaction time in the subsequent trials, as a possible indicator of increased performance following a rewarding stimulus. This analysis yielded a large effect of trial, *est* = −2.26, 95% *CI* = −2.40–−2.11, *t* = −31.14, *p* < .001, showing that, on average, participants improved their reaction times in each trial by 2.26 ms. No other rating significantly predicted reaction times: familiarity (*est* = −0.03, 95% *CI* = −0.25–0.18, *t* = −0.32, *p* = .75), social relevance

(*est* = −0.02, 95% *CI* = −0.23–0.20, *t* = −0.15, *p* = .88), attractiveness (*est* = 0.13, 95% *CI* = −0.11–0.36, *t* = 1.07, *p* = .29), reward value (*est* = 0.06, 95% *CI* = −0.14–0.26, *t* = 0.60, *p* = .55). The overall fit of the model was $R^2_m = 0.37$ and $R^2_m = 1$.

Table 3-9 Exploratory mixed effects models investigating the effects of autistic traits (AQ score) and their interactions with social relevance and familiarity in the game and in the passive viewing task.

	Passive viewing task			**Repeat-a-pattern Game**		
	Est.	*SE*	*t*	*Est.*	*SE*	*t*
Intercept	172.44 (96.13 – 248.74)	38.93	4.43	-992.09 (-1154.76 – -829.41)	83.00	-11.95
Social relevance	-0.10 (-1.25 – 1.06)	0.59	-0.16	0.78 (-0.69 – 2.25)	0.75	1.04
AQ	2.73 (-25.94 – 31.39)	14.63	0.19	-17.11 (-99.74 – 65.53)	42.16	-0.41
Familiarity	0.33 (-0.71 – 1.36)	0.53	0.62	-1.59 (-2.92 – -0.27)	0.68	-2.36
Attractiveness	0.05 (-1.15 – 1.25)	0.61	0.08	1.36 (-0.16 – 2.87)	0.77	1.76
Trial number	-2.15 (-2.98 – -1.31)	0.42	-5.06	0.95 (0.02 – 1.89)	0.48	2.00
AQ x Social relevance	0.02 (-0.56 – 0.61)	0.30	0.07	0.07 (-0.76 – 0.90)	0.42	0.17
AQ x Familiarity	0.43 (-0.02 – 0.88)	0.23	1.86	-0.47 (-1.12 – 0.18)	0.33	-1.43
Game: Reward value				-0.58 (-1.87 – 0.70)	0.66	-0.89
Random Effects						
σ^2	755831.57			1394162.10		
τ_{00}	42239.43 $_{code}$			418152.94 $_{code}$		
	3641.95 $_{item}$					
ICC	0.06			0.23		
N	70 $_{code}$			70 $_{code}$		
	10 $_{item}$					
Observations	6211			6408		
Marginal R^2 / Conditional R^2	0.005 / 0.062			0.004 / 0.234		

P-values are intentionally not provided due to the exploratory nature of the model.
ICC = interclass correlation coefficient
τ_{00} = between-subject-variance

3.3.3.5 Pupillary Responses—Exploratory Analysis with Autistic Traits

We built additional models for each task including the AQ scores and their interactions with the stimuli's familiarity and social relevance to explore their possible effects on the pupillary responses. The models are shown in Table 3-9.

Although autistic traits (AQ score) were not a promising predictor of pupil size in either of the tasks (game: $f_p = 0.05$, passive task: $f_p = 0.02$), the confidence intervals and the standard error for the estimates in the passive viewing task suggest that a noteworthy amount of variance was explained by the AQ × familiarity interaction ($f_p = 0.04$). A visual inspection of this interaction (Figure 3-18) showed numerically larger pupil sizes for higher autistic traits in high familiarity and smaller pupil sizes in increased autistic traits in low familiarity.

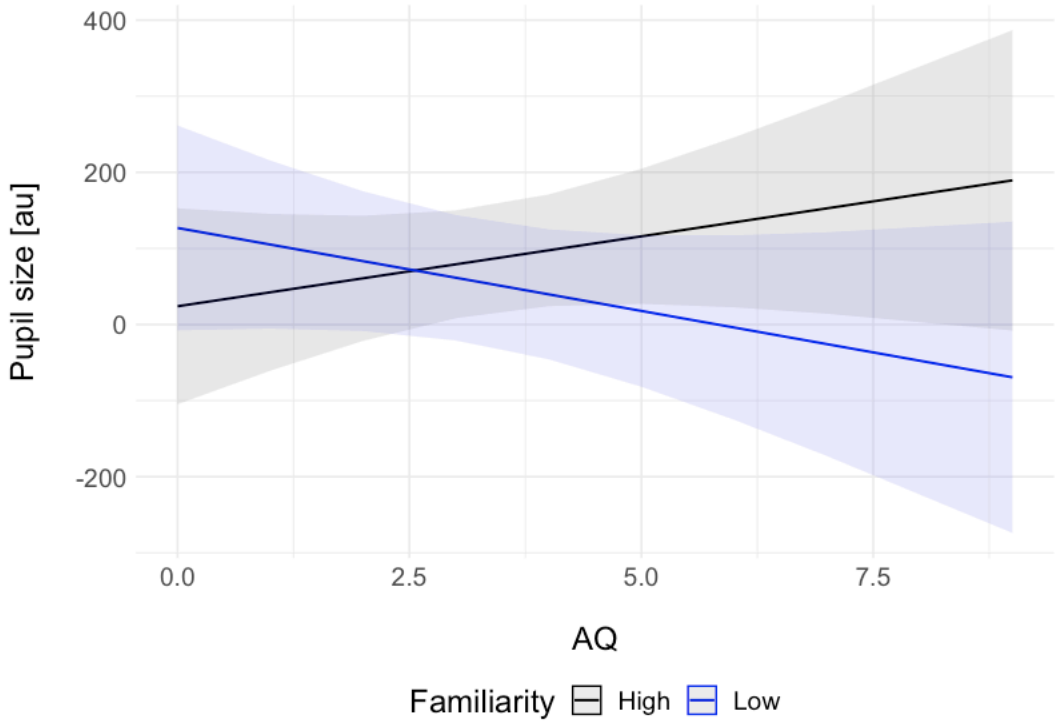

Figure 3-18 Interaction effects of autistic traits (AQ) and familiarity on pupil size in the passive viewing task. For the purpose of visualisation, the continuous familiarity rating was divided into two factors at value 50 (the range was 1 to 101) into low and high familiarity. The grey areas show 95% confidence intervals.

3.3.5 Discussion

In this study, we explored pupillary responses to smiling faces differing in their subjective familiarity, social relevance, and reward value. We considered these faces as social rewards either contingent on behaviour (in a repeat-a-pattern game) or not (in a passive viewing task). To this end, we measured pupillary responses to pictures of smiling faces of strangers (on average rated by the participants as not socially relevant and not familiar), celebrities (non-relevant but familiar) and experimenters (relevant and familiar). We hypothesised that we would observe increased pupil responses in response (1) to more familiar and socially relevant faces and (2) in the repeat-a-pattern game rather than in the passive viewing task. In the passive viewing task, none of the hypothesised predictors showed significant effects, while in the game we unexpectedly observed decreased pupil sizes as a response to more familiar faces. Additionally, the results showed contrasting tonic changes in pupil size in the two tasks: with time (subsequent trials) the pupil size became smaller in the passive viewing task and larger in the game. Reaction times in the game were not modulated by any of the variables of interest. Finally, in an exploratory analysis, we investigated the effects of autistic traits and their interactions with familiarity and social relevance in neurotypical participants in our tasks. As anticipated, we observed that higher autistic traits were linked to smaller pupil sizes when viewing less familiar faces and to larger pupil sizes for more familiar faces.

3.3.5.1 Subjective Ratings of the Familiarity and Social Relevance of the Stimuli

To ensure that the values of familiarity and social relevance in our study are widespread, we created a stimulus set comprising of three basic face types: strangers, celebrities, and experimenters. Strangers are socially non-relevant to the participants, as they share no social context, and unfamiliar, as they have never met. In contrast, experimenters become familiar and socially relevant to the participants in the context of the study and due to the socialising procedure implemented in its design. Finally, the celebrities, although not personally acquainted or relevant, are characterised by a certain familiarity due to media exposure. We collected participants' subjective ratings of social relevance and familiarity of the stimuli (as well as attractiveness and reward value in both tasks). Subjective ratings are a popular method of reflecting qualitative values of stimuli, and are also used for familiarity (Baudouin et al., 2000; Lander

& Metcalfe, 2007). The ratings showed that, on average, the experimenters were indeed perceived as more socially relevant and familiar than the other two faces, and celebrities were also rated as more familiar than strangers. Although the distribution of the ratings showed a considerable intraindividual variability, our results reflected this variance by including subjective ratings as predictors in the planned analyses (for familiarity and social relevance ratings, including raw data points and means, see Figure 3-20 and Figure 3-21 in the supplementary material).

3.3.5.2 Social Reward and Pupillary Responses

Social Relevance

We hypothesised that faces of high social relevance and familiarity would be linked to larger pupil sizes in both tasks, especially in the repeat-a-pattern game. Against our predictions, we observed no effects of social relevance in either of the tasks. One reason for this may be that the experimenters, although significantly more relevant to the participants than celebrities and strangers (as suggested by the subjective ratings), were not relevant enough for the pupillary responses to reflect this effect. Indeed, social relevance has so far been discussed in the context of individuals linked to strong emotional responses, i.e., to loved ones (Sugiura, 2014). Hence, the experimenters might not have been relevant enough to elicit a strong reward-related response. However, since to our knowledge no study has so far linked pupil behaviour to social relevance of faces (and specifically study experimenters), our observation is novel and requires more research to shed light on this interpretation.

Alternatively, the ratings of social relevance and familiarity in our models may in fact have explained similar parts of the overall variance and, by including both terms in the regression analysis, the true effect of social relevance might have been occluded. In such a case, a model without familiarity could reveal a larger estimate of social relevance and should be penalised less for overfitting. This, however, was not the case (for this exploratory testing, see points 4.2.2 and 5.2.2 in the analysis code).

Finally, it is possible that social relevance of a face is simply not a good predictor of its reward value (at least without engagement of strong emotions as is the case for loved ones). Indeed, although in the repeat-a-pattern game the subjective reward value showed correlations with both social relevance and familiarity, this relationship was stronger for the latter. Additionally, self-

rated reward value in the passive viewing task did not correlate with social relevance, even though it did with familiarity. Nonetheless, this result should be viewed with caution, as reward value may not be a meaningful concept in the context of positive stimuli presented in a passive viewing task. This is in line with the otherwise surprising higher 'reward' ratings for the stranger than other faces in this task. Overall, these results suggest that social relevance (at least in the range present in this study) of smiling faces does not play a significant role for the reward value of such stimuli.

Familiarity

Although our analyses revealed an effect of familiarity on pupillary responses, it was only manifested in the repeat-a-pattern game and, in contrast to our hypothesis, showed a negative direction: more familiar faces were linked to smaller pupil sizes. Importantly, previous research has provided similar findings. For example, Schneider et al. (2018) observed greater and longer dilation for no-reward outcomes than for both monetary and non-monetary outcomes (reported in the supplementary material). If, as indicated in the subjective ratings in our study, the experimenters and celebrities were indeed more rewarding than strangers for the participants in the repeat-a-pattern game, our pattern of results (smaller pupils in response to more rewarding outcomes) parallels those of Schneider and colleagues. This, however, stands at odds with previous studies reporting increase in pupil sizes in response to higher magnitudes of rewards (Koelewijn et al., 2018) and addiction-related images (Chae et al., 2008). Notably, in these studies the pupil behaviour was measured in response to an incentive and not to an actually received reward. Given that the neural and behavioural differences between reward anticipation and reception are well established (Berridge et al., 2009), it is possible that the pupil-coded reward reception targeted in our study does not follow the same pattern of responses as in the studies investigating anticipation.

Since neither the subjective ratings of social relevance nor the reward value predicted pupillary responses, our data did not yield evidence for a straightforward relationship between pupil size and reward. Nonetheless, we consider a few interpretations for the role of pupillary responses in social reward processing. One possible explanation for the observed results is that pupil sizes do not actually reflect reward value of a stimulus via arousal, but rather mere physiological arousal (not modulated robustly by the stimulus).

Although we did not directly ask participants to rate their arousal in response to the stimuli, pupil sizes have been repeatedly used as its proxy (Mathôt, 2018). However, this selective interpretation stands in contrast to the growing body of literature utilising pupillometry in reward research (e.g., Cash-Padgett et al., 2018; Chae et al., 2008; Koelewijn et al., 2018; Schneider et al., 2018; Takarada & Nozaki, 2017). Moreover, if the negative relationship of pupil sizes and familiarity in our study was indeed a reflection of reduced arousal to more familiar faces, this contradicts previous reports of familiar faces (especially with happy expressions) judged as more arousing than unknown ones (Dobel et al., 2008).

Alternatively, the pupil may reflect a reward-related mechanism, however, instead of coding the value of a reward (or from a subjective point of view: appreciation of a reward), it rather reflects its motivational power. Indeed, it has recently been proposed that pupils reflect the activity of the LC neurons, which play a significant role in mobilising energy and resources necessary to perform future actions (Bouret & Richmond, 2015). Indeed, in some studies the pupil is found only to be modulated by reward magnitude in difficult tasks, in which recruitment of resources and effort are needed to perform them (Bijleveld et al., 2009). This interpretation is further supported by the fact that the effect of familiarity was observed in this study in the repeat-a-pattern game but not in the passive viewing task. While in the repeat-a-pattern game, after receiving feedback, the participants were preparing to perform again in the next trial, in the passive viewing task no action was required. Under this interpretation, our data suggest that receiving positive feedback from unfamiliar persons mobilises more resources to perform than does feedback from known faces. A tentative reason for this may lie in the desire to perform well in front of persons about whom we cannot be sure whether they have positive or negative attitudes towards us (such as strangers), in contrast to more familiar experimenters, who are known to be pleasant and helpful. While not disputing that this is a possible interpretation of the obtained results, we recognise that our paradigm does not provide a robust support for it and that different designs are needed to specifically tackle this question.

Finally, our results may reflect a link between pupil size and surprise. In this view, the pupil does not reflect expected reward or uncertainty per se, but rather errors in judging uncertainty, i.e., surprise (Preuschoff et al., 2011). Although in our paradigm the different face types were displayed in a random order, it is possible that receiving a smile from an unknown person as feedback

for one's actions is surprising, as it rarely happens in natural situations. Moreover, this interpretation explains the lack of effects in the passive viewing task: as no performance-dependent feedback was included in this task, no surprise could arise, and thus none of the faces were perceived as being more surprising than others.

3.3.5.3 Reward Contingent on Behaviour

In this study, we contrasted two tasks: a repeat-a-pattern game, in which participants were asked to quickly repeat a pattern and then received feedback dependent on their performance, and a passive viewing task, in which no action was required, and participants were only asked to pay attention to the stimuli. The aim was to compare the reward value of positive stimuli serving as feedback (rewards) and positive stimuli presented regardless of one's actions. Importantly, the stimuli (smiling faces) in both tasks were the same for each participant. Thus, the difference in pupil responses to the stimuli between the tasks were essentially due to their contingency on performance (in the repeat-a-pattern game) or lack thereof (in the passive viewing task). We hypothesised that the modulatory effects of the stimuli (i.e., social relevance and familiarity) would be larger in the game. Indeed, familiarity of the smiling faces was a significant predictor of the pupil size in the game, but not in the passive viewing task. We believe that the reason for this is that positive stimuli can be considered to be rewards only when their delivery is contingent on one's behaviour.

Although the ratings of reward value in the passive viewing task should be treated with caution for the abovementioned reasons, a pattern of results emerging from the subjective ratings supports that which is found in the autonomic responses. The reported reward values of the smiling faces were higher in the game and the reward values of the faces correlated positively with social relevance and attractiveness in the game, but not in the passive viewing task. Overall, this suggests that the feedback context (i.e., contingency on behaviour) changes the way social rewards are processed in contrast to passively viewed positive stimuli not contingent on one's behaviour. Additionally, it is worth mentioning that the two tasks in this study were linked to contrasting effects of time. Specifically, in the game the pupil sizes increased over trials and in the passive viewing task, they decreased. The likely reason for these effects is tonic changes in the tasks: the passive viewing task was monotonous and the decreased pupil size over time could reflect

growing fatigue, whereas the repeat-a-pattern game was entertaining and the motivation for performance retained with increasing speed of the pattern presentation over blocks. This possibly led to increased arousal. These effects once again point to the differential engagement in the tasks, and through that with the rewards.

3.3.5.4 Exploratory Analyses

Autistic Traits and Pupillary Responses

In addition to the main hypotheses, we explored the effect of autistic traits on the pupillary responses to smiling faces in both tasks. Autistic traits were not a good predictor of the pupil size in either of the tasks. However, we observed a predicted descriptive interaction of autistic traits and familiarity of the stimuli in the passive viewing task. The higher the autistic traits, the smaller the pupil responses to less familiar faces. This result parallels that of Nuske et al. (2014), who reported reduced pupillary responses to fearful expressions of unfamiliar people (but not familiar ones) in children with ASC relative to typically developing controls. Our exploratory analysis furthers that finding by pointing towards a descriptive effect in a sample of neurotypical subjects differing in the levels of autistic traits. Such results are interesting because they show that social difficulties characterising ASC are likely mediated by the familiarity of others.

Correlations of Attractiveness and Reward Value

It has been suggested that attractive faces can be processed similarly to rewards, and indeed, activation of the reward circuitry in the brain in response to beautiful faces has been previously reported (Aharon et al., 2001). A positive correlation between subjective ratings of familiarity and reward values in our tasks further supports this claim. However, we only observed such a correlation in the repeat-a-pattern game and not in the passive viewing task. This suggests that, at least on the subjective level, attractive faces are indeed perceived as more rewarding when they serve as feedback contingent on behaviour. This correlation, however, should be viewed with a certain degree of caution, as it is based on a relatively small amount of data, and it does not inform about the causality of the relationship between attractiveness and reward.

3.3.5.6 Limitations

This study is not free of limitations. A growing body of literature emphasises the need to increase the ecological validity in experiments by including dynamic instead of static faces as stimuli (Dziobek, 2012). Here, we used static stimuli to ensure higher control over their physical properties, mainly luminance, which is a crucial factor in pupillometry. Nonetheless, to make the social stimuli more naturalistic, dynamic counterparts of pictures of smiling faces should be employed in future studies.

Particular to this study, it should be noted that we only included female faces in the stimuli set. This was done to match the physical gender of the experimenters (two females). However, a replication of our results with a multigender stimulus set is needed before they can be generalised further.

Thirdly, it should be noted that all variables of interest in our models explained a small fraction of the total variance (and thus showed small effect sizes). However, effect sizes in social psychology are commonly smaller than the traditional thresholds for 'small', 'medium', and 'large' effects would suggest (Richard et al., 2003). Moreover, cognitive factors typically explain a strikingly small variance in pupil size in comparison to physiological changes such as blinks or tonic fluctuations (Knapen et al., 2016). Nevertheless, it would be of great benefit to compare our results to similar paradigms employing other psychophysiological indicators of reward processing (e.g., event-related brain potentials).

Fourthly, the subjective ratings of familiarity and social relevance (as well as attractiveness and reward value) were taken at the end of the study, which grasps the final subjective impressions of the participants. Hence, in the unlikely case that the levels of subjective familiarity and relevance changed dynamically throughout the time of the experiment, this might not be reflected in the data.

Finally, despite a growing number of published works exploring pupil behaviour as an indicator of reward processing, this is still a relatively narrow and largely unexplored field. While on the one hand it is difficult to propose convincing interpretations of the results obtained, on the other hand our results emphasise the need to invest more efforts in this research path.

3.3.5.7 Conclusions

This study set out to explore the modulatory effects of familiarity and social relevance of social rewards on pupillary responses in tasks in which the reception of a reward was or was not dependent on one's performance. It provides two major insights. Firstly, familiarity plays a role in the processing of social rewards. Known and unknown faces, regardless of their social relevance, influence the physiological responses to rewarding outcomes differently. Secondly, feedback context is crucial in reward research as positive stimuli are (more) rewarding when they are contingent on behaviour. Both the psychophysiological measurements (pupil dilations) and behavioural responses (subjective ratings) suggested that the feedback context substantially changes how the rewards are processed. The pupil sizes were modulated by familiarity of the rewarding faces only when these faces followed a successful performance. Overall, the findings of this study contribute to our understanding of the social reward processing by targeting the crucial components of the human socio-cognitive functioning: familiarity and social relevance.

3.3.6 Supplementary material

Table 3-10 Pairwise comparisons for the effect of face type on the subject ratings of reward value in both tasks (with Holm correction)

Contrast	*Est.*	*SE*	*z*	p_{corr}
celebrity.Game - stranger.Game	10.114	4.298	2.353	0.129
celebrity.Passive_task - celebrity.Game	-12.014	3.959	-3.035	0.019
celebrity.Passive_task - stranger.Passive_task	-26.886	4.298	-6.255	<0.001
experimenter.Game - celebrity.Game	20.714	4.771	4.342	<0.001
experimenter.Game - stranger.Game	30.829	4.112	7.497	<0.001
experimenter.Passive_task - celebrity.Passive_task	-3.186	4.771	-0.668	0.979
experimenter.Passive_task - experimenter.Game	-35.914	3.959	-9.072	<0.001
experimenter.Passive_task - stranger.Passive_task	-30.071	4.112	-7.313	<0.001
stranger.Passive_task - stranger.Game	24.986	3.959	6.312	<0.001

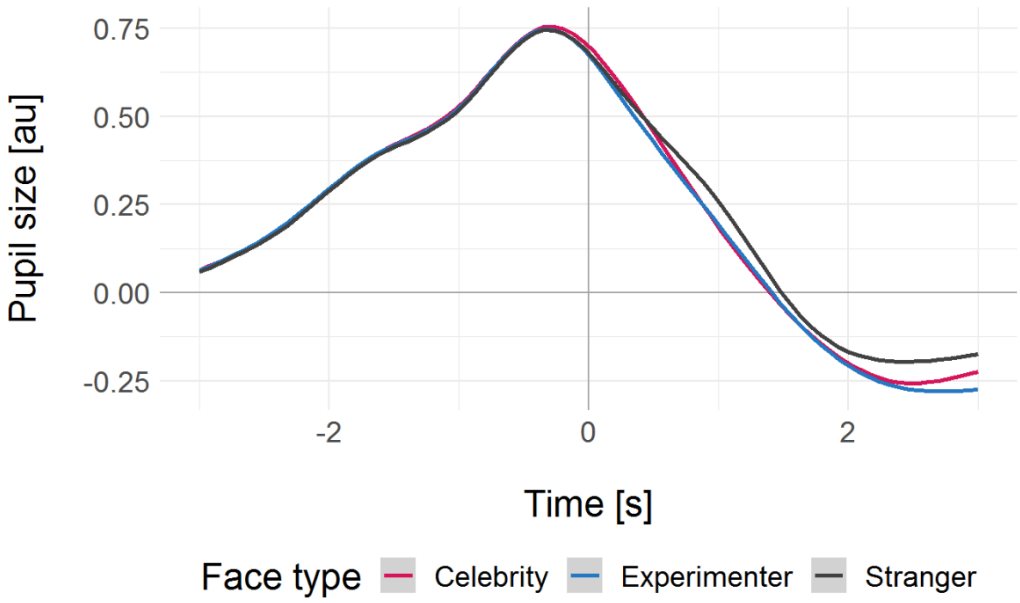

Figure 3-19 Plot of the pupillary responses across face types in the game - time-locked to the onset of the face presentation.

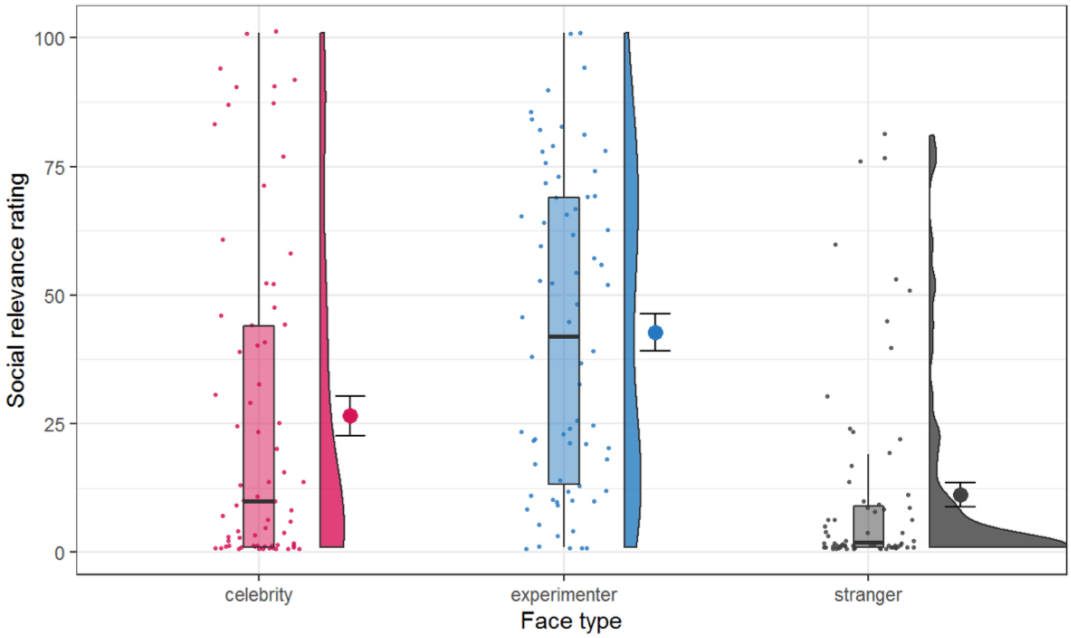

Figure 3-20 Subjective ratings of feedback's social relevance in the game and the passive task. The plot portraits: raw data points, boxplot, violin plot, and means with error bars marking standard deviation.

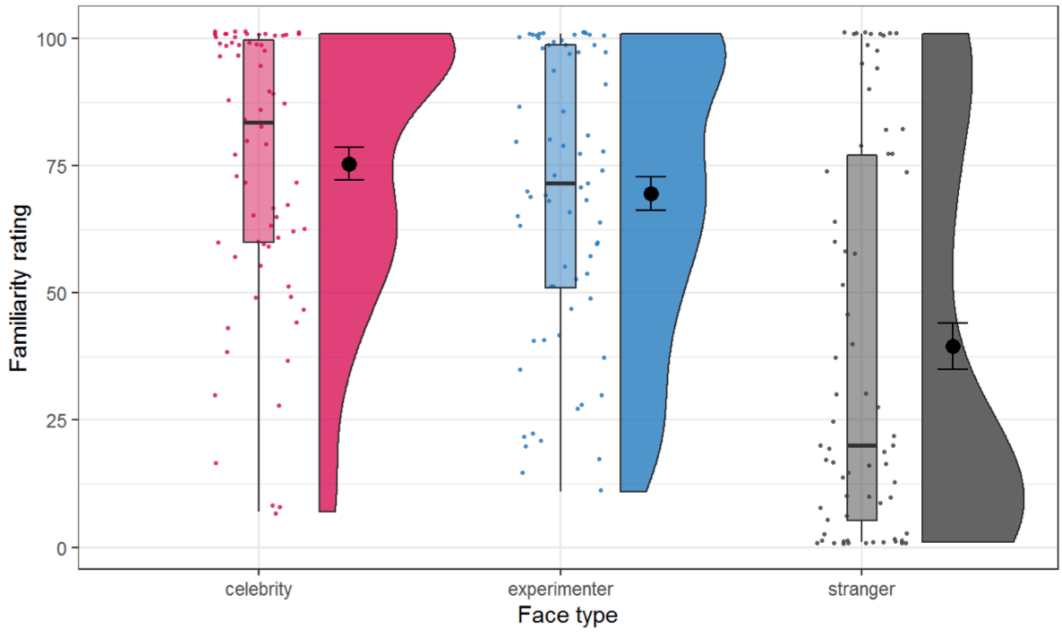

Figure 3-21 Subjective ratings of feedback's familiarity in the game and the passive task. The plot portraits: raw data points, boxplot, violin plot, and means with error bars marking standard deviation.

3.4 Study 4: Multidimensionality of rewards

A Multidimensional View on Social and Non-Social Rewards

Magdalena Matyjek, Stefanie Meliss, Isabel Dziobek, & Kou Murayama

Abstract Social rewards are a broad and heterogeneous set of stimuli including for instance smiling faces, gestures, or praise. They have been widely investigated in cognitive and social neuroscience as well as psychology. Research often contrasts the neural processing of social rewards with non-social ones, with the aim to demonstrate the privileged and unique nature of social rewards or to examine shared neural processing underlying them. However, such comparisons mostly neglect other important dimensions of rewards that are conflated in those types of rewards: primacy, temporal proximity, duration, familiarity, source, tangibility, naturalness, and magnitude. We identify how commonly used rewards in both social and non-social domains may differ in respect to these dimensions and how their interaction calls for careful consideration of alternative interpretations of observed effects. Additionally, we propose potential solutions on how to adapt the multidimensional view to experimental research. Altogether, these methodological considerations aim to inform and improve future experimental designs in research utilizing rewarding stimuli, especially in the social domain.

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3.4.1 Social and Non-Social Rewards

Rewards are desired, appetitive, and positive outcomes of motivated behaviour that can increase and maintain the frequency and strength of the behaviour they are contingent on (Schultz, 2015). They often serve as reinforcers, i.e., positive (or in other cases negative) stimuli or events that actually change the probability of that behaviour's occurrence or its strength in the future (Tobler & Kobayashi, 2009). Because humans do not live in isolation, many rewarding experiences stem from social interaction and relationships.

Social rewards are a broad set of stimuli, which instigate positive experiences involving other people, including a vast repertoire of verbal and non-verbal behaviors, gestures, and feelings (Bhanji & Delgado, 2014) such as a smile (Spreckelmeyer et al., 2009), praise (Deci, 1971), a thumbs-up (Oumeziane et al., 2017), acquisition of good reputation (Izuma et al., 2008), etc. However, despite the considerable heterogeneity of social rewards and abundance of research utilizing them, it is not clear what constitutes rewards as social and there has been surprisingly little systematic discussion on how we can conceptualize them. Nevertheless, regardless of lacking a clear definition of social rewards, there is a large body of literature discussing them in relation to non-social ones.

Social rewards have been studied by two different lines of research. The first line of research aims to address the 'privileged' nature of social rewards, arguing that there are dedicated, special mechanisms that subserve social functioning, including social rewards. These studies often contrast them against non-social rewards to demonstrate if and how they are processed differently from non-social environmental rewards. For example, autism, which is characterized by pervasive social impairments (American Psychiatric Association, 2013), has been taken as an example of atypical responsiveness to social cues. Researchers have hypothesised impaired processing of social, and preserved processing of non-social rewards (social motivation hypothesis; Chevallier et al., 2012) and have been testing this prediction by comparing responses to social and non-social rewards (for a review, see Bottini, 2018). The comparison is also common in other fields with non-clinical populations (e.g., Kohls et al., 2009).

Another line of research has indicated that social and non-social rewards may be processed in a similar manner. This is supported by economic theories proposing that behaviours stem from the desire to maximize the ratio of rewards to costs (Von Neumann & Morgenstern, 1947) and this applies to non-social as well as to social rewards (social exchange theory; Thibaut & Kelley, 1959). Indeed, many studies investigating the neural basis of reward processing found that social and non-social rewards are processed in the same brain areas of what is referred to as the reward network (i.e., a cortico-basal ganglia circuit; Haber & Knutson, 2010), especially in the striatum, supporting the assumption of an 'extended common currency schema' (Ruff & Fehr, 2014). However, researchers have also emphasized specific activity differences in line with the idea of 'social-valuation-specific schema' (Ruff & Fehr, 2014),

which assumes dedicated brain circuits for social rewards. For instance, a study comparing the rewarding properties of receiving money or positive social feedback found that both rewards activated the striatum, especially the left nucleus caudate, and that this region also showed a linear activity increase towards both reward values (Izuma et al., 2008). A reanalysis of the same data using machine learning, however, yielded a fairly small correlation between classifier weights for social and monetary rewards, suggesting that only a subset of neurons in the caudate nucleus encodes both rewards, whereas also distinct populations of neurons are involved for social and for non-social rewards separately (Wake & Izuma, 2017). Thus, although both types of rewards can be processed in similar structures of the reward network in the brain (Izuma et al., 2008; Levy & Glimcher, 2011; Lin, Adolphs, et al., 2012; Smith et al., 2010; Spreckelmeyer et al., 2009; Wake & Izuma, 2017), there has also been accumulating evidence for differences in neural processing between social and non-social rewards (e.g., Izuma et al., 2008; Sescousse et al., 2010; Smith et al., 2010; for a recent review of literature discussing overlaps and differences in neural processing of social and non-social rewards, see Ruff & Fehr, 2014).

These studies suggest that there are both similarities and differences in neural processing between social and non-social rewards. However, we argue that research comparing social and non-social rewards often neglects important dimensions that can be conflated with the sociality dimension. For example, comparing brain responses to receiving a smile or money may potentially reveal a difference between social and non-social rewards as well as between intangible and tangible rewards. In this article, we propose a more comprehensive, multidimensional view on rewards in experimental settings, which allows more informed and better-controlled comparisons of social and non-social rewards.

3.4.2 Dimensions of Rewarding Stimuli

Research contrasting social and non-social rewards implicitly assumes a binary categorization of those rewards. However, monetary reward is considered as non-social, but money could be regarded as a "social construct" in the sense that it would not exist without society and a collective agreement of their function (social constructionism; e.g., Galbin, 2014). Thus, binary categorization of social and non-social may be an oversimplification, and a continuous dimension may provide a more accurate conceptualization. Moreover, we suggest that there are other dimensions to describe rewards,

e.g., tangibility and primacy, and that considering them can offer alternative interpretations of observed differences between social vs. non-social rewards. This section describes these dimensions of rewarding stimuli (see Figure 3-22 for an overview). Our goal is not to provide a complete list of all possible dimensions, but to outline the scope of this multidimensional view with several examples, which we consider particularly relevant for social vs. non-social reward processing: primacy, temporal proximity, duration, familiarity, source, tangibility, naturalness, and magnitude. Importantly, we discuss how each of these dimensions interacts and confounds with social vs. non-social dimension.

3.4.2.1 Primacy

Primacy is a dimension categorizing rewards (after theories of operant conditioning; Skinner, 1938) depending on whether they stem from innate or biologically pre-programmed reinforcing states (hunger satisfied by food or mother's closeness satisfying the need for touch of an infant) on one hand (i.e., primary rewards), or having rewarding properties through learned or acquired associations with primary reinforcers (money as a means to acquire food, a Facebook thumbs-up to gain social appreciation) on the other hand (i.e., secondary rewards; Delgado et al., 2006). Thus, primary and secondary rewards can be found in both, social (touch, thumbs-up) and non-social (food, money) domain. Studies have shown that even though there is a partial overlap in the ventromedial prefrontal cortex (vmPFC) representing the anticipatory value of primary and secondary rewards (Kim et al., 2011; Levy & Glimcher, 2011), there is also additional activity specific to primary (i.e. hypothalamic regions) and secondary rewards (i.e., posterior cingulate cortex; Levy & Glimcher, 2011), respectively. Since primacy can be linked to distinct neural processing, it is important to choose rewards of the same primacy nature when comparing social and non-social ones.

3.4.2.2 Temporal Proximity

Temporal proximity describes the temporal relationship between motivated behaviour and reward reception (e.g., immediate vs. delayed). There is evidence that they are processed distinctly in the human brain (e.g., Ballard & Knutson, 2009; for a review, see Bermudez & Schultz, 2014). Specifically, midbrain, striatum, frontal cortex, and amygdala are all sensitive to time of reward

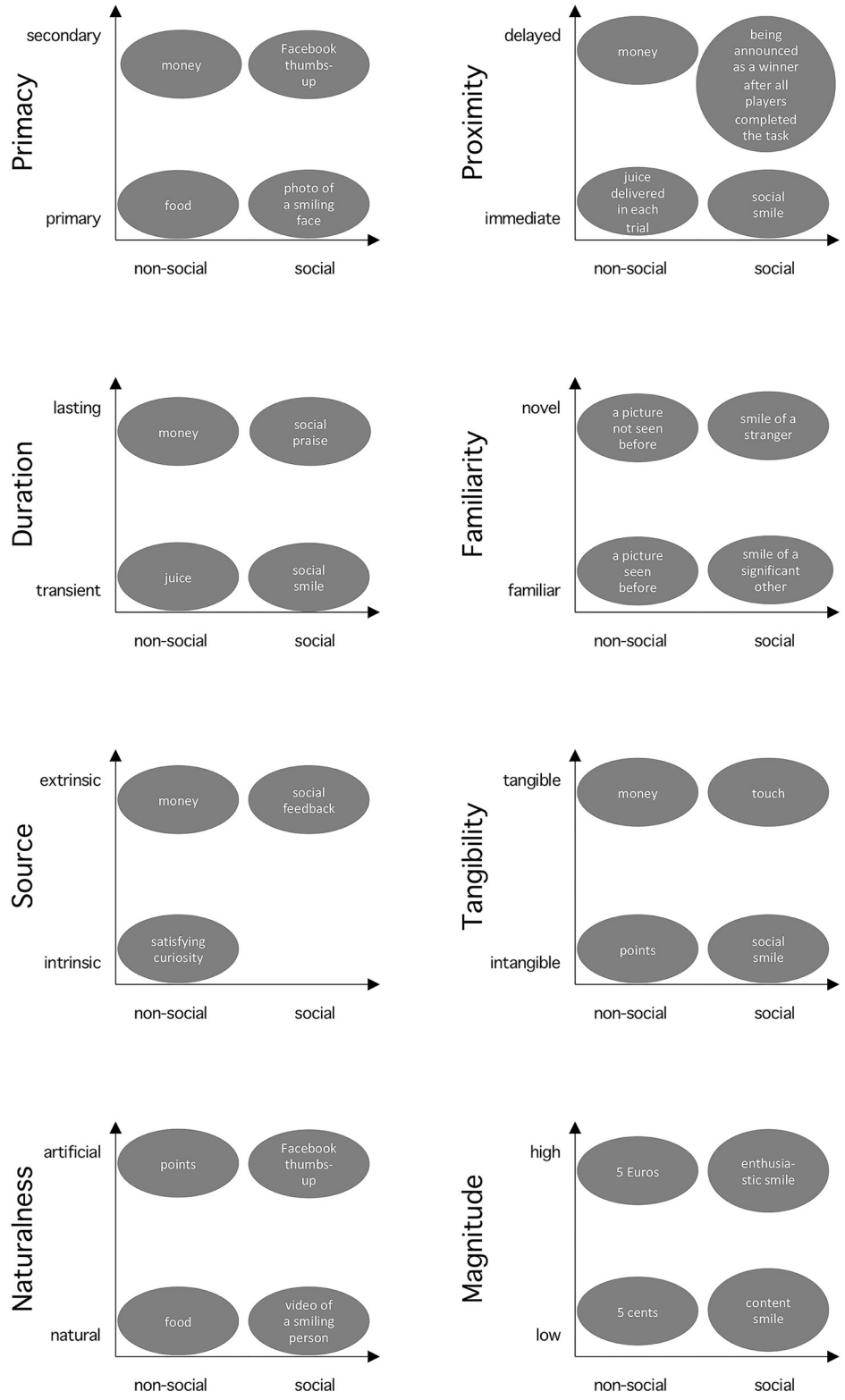

Figure 3-22 Interplay of the sociality and other reward dimensions. The x-axis represents the sociality dimension. The provided cases illustrate examples of rewards used in psychology and neuroscience placed along the dimensions discussed in this article. The spatial distance between the cases does not directly depict differences in their rewarding value.

occurrence (soon or later). Moreover, temporal discounting may lead to a preference for sooner smaller compared to later larger rewards. Social rewards are usually delivered immediately at the end of the trial in the form of a smile or social feedback, aligning simultaneous reception and consumption of reward. However, in the non-social domain, there is often a difference between reward reception in an experimental trial (e.g., a picture of a coin) and the actual consumption of the reward after the experiment (i.e., receiving the physical money). Note that sometimes the amount of points won in trials is not even directly translated to actual money gains (O'Doherty et al., 2001). Thus, comparing social rewards with non-social rewards may trigger brain responses reflecting differences in the temporal proximity dimension in addition to the sociality dimension.

3.4.2.3 Duration

The dimension of duration distinguishes between lasting and transient rewards. Unlike transient rewards (consumed/appreciated while presented), lasting ones may entail accumulation over time, which affects economic decision making and activity in vmPFC (Juechems et al., 2017). While social ones most often are transient (a smile lasts only while presented, but praise may have longer-lasting effects generating feelings of appreciation), non-social rewards are more dependent on the experimental context. For example, money received in a task is still available after the end of the experiment, whereas juice delivered on a trial-by-trial basis is immediately consumed. Thus, when comparing social and non-social rewards, duration needs to be considered to avoid confoundedness.

3.4.2.4 Familiarity

Familiarity differentiates novel from familiar stimuli and is signalled in the striatum and the midbrain (Guitart-Masip et al., 2010). While novelty is rewarding in non-social stimuli (Guitart-Masip et al., 2010), it may be the opposite in the social domain, where familiar and socially relevant faces are more rewarding than faces of strangers (Pankert et al., 2014). In fact, it has been shown that familiar faces are processed differently than faces of unknown people, due to different visual representations stored in memory, personal knowledge, and personal relevance (Ramon & Gobbini, 2018). Furthermore, "familiarity" in the context of social rewards has multi-faceted meanings and there may be qualitative differences between familiarity with relatives,

celebrities, and experimentally learned individuals (Ramon & Gobbini, 2018), which can potentially lead to inconsistencies through differential engagement in experimental tasks (Liccione et al., 2014). Altogether, familiarity may modulate social and non-social rewards differently, which should be considered in study designs.

3.4.2.5 Source

Source relates to whether the rewarding nature originates internally (i.e., intrinsically within a person, e.g., feeling curious) or externally (i.e., extrinsically by receiving food or praise). While psychological theories consider them as distinct (e.g., Deci et al., 2001), neuroscientific studies show that rewards from both sources activate the reward network (Murayama, 2019), with additional brain regions specific for intrinsic rewards (the anterior insula; Lee, 2016). This can be a potential confound for the sociality dimension, as non-social rewards could stem from both sources (satisfying curiosity or receiving money), but social rewards are by definition extrinsic as provided by others (e.g., social feedback).

3.4.2.6 Tangibility

Tangibility refers to the property of a stimulus to be touched or consumed, with more abstract stimuli being less tangible. Studies suggest differential reinforcing and motivating effects of tangible and intangible stimuli (Yoon et al., 2015), often via differential engagement of intrinsic and extrinsic motivation (Deci et al., 1999). For example, in a study with tangible monetary and intangible verbal rewards on intrinsic motivation, only the latter showed positive and prolonged effects (Albrecht et al., 2014). Because social rewards are most often intangible (like verbal praise) and non-social rewards are tangible (e.g., money), the interaction of sociality and tangibility is a potential confound.

3.4.2.7 Naturalness

Some studies use natural stimuli such as chocolate (Levy & Glimcher, 2011) or verbal praise (Warneken & Tomasello, 2008) as rewards, whereas other studies use more arbitrary, symbolic stimuli such as Facebook thumbs-up icon (Oumeziane et al., 2017) or a picture of a coin (Kohls et al., 2009). Naturalness is especially important for social rewards. For example, there is an increasing number of studies using avatars (e.g., Kim et al., 2015) and cartoon

representations of faces (Gonzalez-Gadea et al., 2016), which convey the social nature through the resemblance to their natural equivalences (faces). In fact, computer-generated and natural faces have been shown to elicit similar emotional processing in the amygdala, but also differential activation in the fusiform face area (Kätsyri et al., 2020). Again, the interaction of sociality and this dimension should be considered and controlled for by choosing both social and non-social rewards to be either natural or representational.

3.4.2.8 Magnitude

The magnitude of a reward can be defined as the extent of its objective and subjective value. Studies have shown that activity in the ventral striatum correlates with the objective magnitude of both monetary (increasing amounts; Knutson et al., 2001) and social rewards (happy face expressions with increasing intensity level; Spreckelmeyer et al., 2009), and vmPFC correlates with the subjective magnitude of rewards (Lin, Adolphs, et al., 2012). Critically, rewards with higher magnitude are likely to elicit larger responses in wider areas of the brain in comparison to rewards with lower magnitude (Diekhof et al., 2012; Smith et al., 2009). Differences in magnitude between rewards should thus be avoided to allow interpretation of the observed effects in terms of social vs. non-social (and not low vs. high magnitude).

In addition to the dimensions above, some other aspects contrast social rewards against other rewards. For example, social stimuli are usually complex and can be more ambiguous than non-social ones: The same smile may be interpreted as a friendly reaction or as a ridicule, depending on the context. Thus, it is important to take into account biases in the interpretation of ambiguous social stimuli linked to internal states (e.g., negativity bias in depressive states; Baumeister et al., 2020). Also, psychological traits and conditions (like autistic traits and social anxiety; (Cox et al., 2015; Cremers et al., 2015), respectively) have been shown to modulate responses to social rewards specifically. Likewise, visual complexity may introduce altered processing: Non-social rewards are often less visually complex than their social counterparts (Ethridge et al., 2017; Oumeziane et al., 2017), introducing a perceptual bias and neural differences (Pfabigan et al., 2019). Furthermore, it may be more challenging to uniformly induce a rewarding value of social stimuli than of non-social ones, as the rewarding value of social stimuli depends on a certain context around participant and reward. In fact, a smiling face seen on the screen can be

rewarding for a participant performing a task only when they believe to some extent that this smile is contingent on their action, as it happens in natural interactions. Simply instructing participants that a smiling face indicates positive feedback might not make it sufficiently socially rewarding; this requires a perceived social context between the participant and the person on the screen, entailing that "social interaction must not inherently be rewarding due to the appearance of positive social stimuli" (Krach et al., 2010, p. 1). Although some studies suggest that bottom-up processes are involved in the privileged processing of social stimuli (Pfabigan & Han, 2019), for a stimulus to be socially rewarding, it is not enough to be a representation of human likeness/gesture carrying positive feedback. Social rewards require the component of intention and direction from the observer to the observed, even if there is no direct (face-to-face) interaction between those two. In fact, one could consider social rewards that are delivered without a social visual stimulus. For example, in Kujawa et al. (Kujawa et al., 2014) participants saw a green checkmark (abstract symbol) as signifying social acceptance, a salient social reward (Saxe & Haushofer, 2008). This is especially important considering recent attempts to bring experimental research closer to reality, which includes the use of dynamic stimuli (Dziobek, 2012; Hasson et al., 2004) and implementing a second-person approach in (neuroscientific) research on social cognition (Schilbach et al., 2013). Although instantiating social context may come at the cost of losing experimental control, some promising designs aiming to ensure ecological validity and experimental control have been proposed (e.g., Drimalla et al., 2019).

3.4.3 Implications of the Multidimensional View on Rewarding Stimuli in Experimental Designs

As discussed, rewards can be described on multiple dimensions and each of them can be linked to different neural correlates and psychological processes. Thus, research interested in comparing social against non-social rewards should carefully control for other dimensions that may conflate the dimension of interest instead of ascribing the observed effects to a single one, like sociality. However, research has rarely considered these additional aspects of rewards (but see the discussion of primacy and tangibility of money and juice, Kim et al., 2011; or praise, Wake & Izuma, 2017). For example, many studies simply compare smiling faces and monetary outcomes to examine the differences of social vs. non-social processing (Kohls et al., 2011, 2013, 2018;

Richey et al., 2014). However, both outcomes differ not only on the social – non-social dimension, but also in terms of their 1) tangibility: a smile is not tangible, but money as a reward in the form of coins and notes is; 2) primacy: a smile is a primary reward[4], money is secondary; 3) proximity and duration: a smile is immediate and transient (its rewarding value lasts as long as its exposure), whereas money is lasting and distant, as it will be delivered at the end of the experiment. Hence, from this multidimensional perspective observed differences between responses to smiles and money cannot be fully ascribed to the social vs. non-social contrast but could also stem from differences in tangibility, primacy, proximity, and duration.

How can empirical research overcome these potential limitations? One strategy is to incorporate these dimensions as additional factors in an experimental design (e.g., visual complexity in Pfabigan et al., 2019). However, this exponentially increases the number of conditions, which substantially boosts the length of the experiment and/or required sample size. An alternative solution is to use stimuli that match in other dimensions than sociality as much as possible. Previous research has shown that pleasant odours can engage the reward circuits (Bragulat et al., 2010; Jiang et al., 2015; O'Doherty et al., 2000) which could be used in a comparison with social rewards like smiling faces. Both rewards would be balanced in terms of temporal proximity (both immediate), tangibility (both intangible), source (both external), and they can be matched with respect to their primacy, duration, familiarity, naturalness, and magnitude. Another approach could be to condition social and non-social rewards with neutral stimuli. For instance, Lehner et al. (Lehner et al., 2017) matched reward magnitude of chocolate, money, and social smile with thumps-up using a willingness-to-pay paradigm and later paired them with neutral stimuli (matched in colour, luminance, and complexity) to then measure the response to those stimuli. Finally, another potential solution would be to assess other dimensions as much as possible (e.g., using subjective ratings) and statistically control for these effects in the analysis. This strategy can also address potential individual differences in the interpretation of social stimuli.

Another implication of this multidimensional view is noteworthy for one of the most widely-used paradigms that compare social and non-social rewards: Monetary (MID; Knutson et al., 2000, 2001) and Social (SID;

[4] In this article, we consider smile as a primary reward as suggested by infants' preference for smiling faces (Farroni et al., 2007), but other interpretations are possible.

Spreckelmeyer et al., 2009) Incentive Delay tasks. In these tasks, participants are presented with a cue indicating possible outcomes in a given trial: a gain or loss, or no outcome (control condition). After a variable anticipation delay, they perform a task after which feedback (i.e., the amount of reward or punishment) is delivered depending on participants' performance. An advantage of the incentive delay paradigm is that it allows targeting both reward anticipation triggered by an incentive cue indicating a possible future reward, and reward reception, elicited with a rewarding stimulus after task performance (Knutson et al., 2000, 2001). It has been shown that both phases (anticipation and reception) involve different brain regions and they are modulated differently by the domain of rewards (social and non-social), with reception being more domain-specific than anticipation (Rademacher et al., 2010). This paradigm has intuitive appeal to contrast social and non-social rewards, but our multidimensional view suggests the potential difficulty in interpreting the results in terms of anticipation and reception, especially in the context of comparing social and non-social rewards.

For example, Kohls et al. (2011) used a picture of a smiling face as both incentive cues and rewards in the SID task. However, a smile is an immediate reward (participants are being smiled at the moment), which entails that as an incentive cue it triggers not only anticipation as intended, but also reception of this reward. Moreover, in the MID task, a picture of a coin is normally presented as a signal that the trial was successful and thus participants receive a monetary reward. However, in reality, participants receive physical money at the end of the experiment, not immediately after each trial (money is a distant reward in such settings). Hence, a picture of a coin intended to represent a reception of reward may actually trigger another anticipation. In other words, when considering the dimension of temporal proximity, for both cases, the distinction between the reward processing phases becomes rather arbitrary. Confounding these two factors (reward processing phases and domain) has serious consequences on how we should interpret the results because both phases are associated with distinct brain areas (Liu et al., 2011). Disentangling of those factors could be achieved by using neutral, non-rewarding incentive cues to trigger anticipation (e.g., Matyjek, Bayer, et al., 2020), or by matching social and non-social rewards on the temporal proximity dimension (i.e., immediate vs. delayed rewards). For instance, to match social rewards, which are often immediate (e.g., a smile), their non-social counterparts can be delivered on a trial-by-trial basis, e.g., in form of juice (Kim et al., 2011) or direct online

bank transfers. Similarly, to match non-social rewards, which have often delayed reception (e.g., money), the social condition could include trial-by-trial symbolic indications of positive feedback, which translate into social appreciation at the end of the experiment in a form of positive adjectives describing the participant (Izuma et al., 2008), given by an "observer".

At a broader level, one important implication of the proposed multidimensional perspective is that it highlights a more nuanced relationship between social and non-social rewards than what researchers have previously assumed. As indicated earlier, while many studies seek neural correlates specialized to social processes, another body of literature focuses on the similarities among different types of rewards (including social), suggesting that there is a common valuation network in the brain. These two lines of research seem contradictory: One argues that social and non-social rewards are different and the other suggests that they are the same. However, the proposed multidimensional view provides a simple integration (see also Murayama, 2019, in the context of the distinction between intrinsic and extrinsic rewards). While social and non-social rewards are both reinforcers with the potential to guide behaviour, their differential effects are (at least in part) attributable to properties on other dimensions on which rewards can be described (e.g., temporal proximity, familiarity, etc.). Using the multidimensional view as a starting point, we can thoroughly reflect upon mechanisms underlying the processing of social rewards, being able to go beyond the simple assertion that social rewards and non-social rewards are either similar or different.

4

Discussion and insights

This chapter discusses the original work in this dissertation and provides insights for the fields of autism, reward, and social neuropsychology.

4. Discussion and insights

The overall aim of this doctoral project was to elucidate the processing of social and non-social rewards particularly in relation to autism and autistic traits. While a better understanding of this topic has the potential to be remarkably beneficial for the advancement of ASC research as well as clinical interventions, it is empirically challenging: Reward processing is a multifaceted function and autism is a complex condition characterised by a considerable heterogeneity of symptoms. In this dissertation four studies were conducted to contribute to our understanding of reward responsiveness, especially in autism and autistic traits.

In this chapter, I summarise the results of the original works conducted in this dissertation, and I discuss them along three main foci: 1) insights for autism research, 2) insights for reward research, and 3) insights for the field of social neuropsychology.

4.1 Summary of results

In the introduction, I proposed that the following crucial aspects in reward responsiveness in autism are insufficiently or inconsistently addressed in the literature: 1) disentangling and investigating the reward processing phases, i.e., anticipation and reception, while appreciating the potentially dynamic character of the first, 2) addressing the role of familiarity in the processing of social rewards, especially in the context of autism, 3) recognising the difference between 'active' and 'passive' rewards, and 4) investigating reward processing in relation to autism by targeting autistic traits in diagnosed individuals and in the general population, thus offering a broader picture of the reward function in the autism spectrum. Studies 1, 2, and 3 were designed to address those aspects and they constitute the empirical basis in this dissertation. Study 4 is a theoretical perspective on the multidimensionality of rewards and a result of the many insights generated during the empirical work.

4.1.1 Effects of autism and autistic traits

Studies 1 and 2 investigated anticipation and reception of social and non-social rewards by indexing their behavioural and biomarkers (EEG and pupillometry) across autistic traits in neurotypical individuals (population-based approach) and in autism (psychopathological approach). Across all subjects, social and monetary rewards consistently increased behavioural, neuronal, and autonomic responses and were rated as more rewarding and motivating than neutral outcomes. In the next sections, I elaborate on these effects in relation to autism and autistic traits.

4.1.1.1 EEG and autonomic data

In line with the social motivation theory, in the first study we expected that higher autistic traits would be linked to a deficit in specifically social reward processing (indexed by decreased ERP amplitudes). However, we found that higher trait levels in the general population were linked to *enhanced* brain responses (i.e., increased CNV amplitudes) in the early anticipation of both social and non-social rewards. We found no effects of the trait level in the late anticipation or in reception of rewards.

Similarly, in Study 2 we observed enhanced early anticipatory ERP responses (the CNV) for the ASC group in comparison to subjects with low levels of autistic traits and no differences between these groups in late anticipation or reception. In the population-based approach, there were no group effects in either of the processing phases, although higher levels of autistic traits were descriptively linked to larger brain responses in the early anticipation (in line with the population-based result in Study 1 and the psychopathological result in Study 2). In addition to the ERPs, in Study 2 we also investigated pupillary responses as an index of the LC activity related to higher rewarding and motivational values of the incentives. These data showed group differences only in reception and regardless of the reward type: Larger pupil responses (enhanced constrictions) were found in subjects with ASC compared to those with low levels of autistic traits. Importantly, by exploring autistic traits as continuously distributed in the population, we showed that reward processing atypicalities are likely linked to these traits in a linear manner: the higher the autistic traits, the more enhanced the reward-related responses.

4.1.1.2 Behavioural data

In both experiments, autistic traits in subjects not diagnosed with autism influenced neither the ratings of the importance of reward type, nor the motivational and rewarding values of the stimuli. In Study 2, in comparison to subjects with low levels of autistic traits, the ASC group showed lower ratings of how important the reward type in a trial was, how motivating the cues were, and how rewarding the feedback stimuli were. Moreover, in both studies autistic traits correlated negatively with the behavioural approach system scores and positively with behavioural inhibition scores (the BIS/BAS scales), suggesting that the traits are linked to decreased motivation towards rewards, but increased motivation away from punishments. Altogether, self-reported evaluations suggest that reward responsiveness in individuals with ASC is diminished in comparison to individuals with low levels of autistic traits. These data allowed us to interpret the neuronal and autonomic results in the light of quantitative behavioural indexes of reward responsiveness.

Finally, reaction times corrected for accuracy did not differ between the groups in Study 2 (not targeted in Study 1), which is in line with many previous works (Baumeister et al., 2020; Greene et al., 2020; Kohls et al., 2013, 2018; Kohls, Thönessen, et al., 2014; Neuhaus et al., 2015; van Dongen et al., 2015). However, while the responses were faster for monetary than social and neutral outcomes across all groups, both the neuronal and pupillary responses were consistently the largest for the social rewards. These results suggest that behavioural performance (i.e., reaction times) may not be appropriate to reflect autism-related effects on reward processing and they may emerge from different processes than those indexed by the psychophysiological responses.

4.1.1.3 Interpretation

Together, the results of Study 1 and 2 provide evidence for atypical processing of rewards in autism regardless of the domain (social or non-social). In the light of reduced self-reported behavioural reward responsiveness and comparable reaction times in the task for all participants, this suggests that the group differences found in the EEG signals and pupil sizes may reflect compensatory brain mechanisms which result in successful behavioural performance (Shafritz et al., 2015). These results are at odds with the social motivation theory, which predicts that autism is related to deficits specifically in the social domain.

This should be viewed in the light of two important aspects of the experimental designs of Study 1 and 2, which are fairly unique in the field. First, to create a meaningful social context and to address the potentially confounding effect of aberrant processing of unfamiliar faces in autism (Pierce et al., 2004; Pierce & Redcay, 2008), we used pictures of a familiar and socially relevant person (the main experimenter). Second, because social anxiety is a common comorbidity of autism (Bejerot et al., 2014; White et al., 2009) and it has been shown to modulate reward responsiveness (Richey et al., 2014), we controlled for these traits in our statistical analyses. Therefore, our results reflect autism-specific (free from the comorbid influences of social anxiety) effects to meaningful social rewards.

4.1.2 Effects of familiarity and rewarding context

In Study 3, we investigated the role of familiarity and personal relevance in the processing of facial social rewards indexed by pupil size. Because 'active' and 'passive' rewards may be qualitatively different, participants were viewing the smiling faces either actively, i.e., as positive feedback after performing a task (rewarding context), or passively (in the absence of any action). We used three types of faces to cover different levels of familiarity and relevance: experimenters, celebrities, and strangers. Based on participants' ratings, experimenters and celebrities were more familiar than strangers, and experimenters were also more socially relevant than the other two. In the active task, experimenters were also rated as the most rewarding types of faces, followed by the celebrities. The ratings of familiarity and social relevance were further used as predictors of the pupillary responses.

The pupil responses were modulated by familiarity (larger constrictions for more familiar faces), but not by social relevance, and only in the active task. Reaction times in the active task were similar for all stimuli. Therefore, both familiarity and the rewarding context ('active' vs. 'passive' task) play a role in the processing of facial social rewards on an autonomic but not behavioural level. Since the pupil dynamics reflect the activity of the LC (Aston-Jones et al., 1999; Bast et al., 2018; Bouret & Richmond, 2015), these results may indicate that the brain distinguishes acquired rewards from merely positive stimuli and that feedback from persons we know is processed differently than that from strangers. In an exploratory analysis we observed a descriptive interplay between autistic trait levels and familiarity.

The results from this experiment support our interpretation of increased reward value of the social feedback from the experimenter (who is a familiar and, to an extent, a relevant person for the participants) in Studies 1 and 2. Moreover, they reinforce that the same stimuli are differently rewarding when they are *earned* in comparison to when they are passively viewed without any action. Finally, the exploratory analysis in this experiment directly suggests that autistic traits may have different effect on responsiveness to familiar and unfamiliar social rewards.

4.1.3 Multidimensionality of rewards

Although a popular reward dyad in experiments is a picture of a smile and a picture of money (also in Studies 1 and 2 in this dissertation), it may be an oversimplification to interpret and generalise observed differences between responses to these two as the effect of sociality (social vs. non-social). Building on the insights I acquired while planning and conducting the empirical studies, together with co-authors we constructed a theoretical perspective which proposes a larger framework for understanding and working with multidimensionality of rewards.

In this perspective, we argue that rewards can be described on many other dimensions than sociality. These are, among others, primacy, temporal proximity, duration, familiarity, source, tangibility, naturalness, and magnitude. Importantly, we present empirical evidence for modulatory effects of each of them on cognitive, behavioural, or neuronal processing and we show how they interact with the sociality dimension. For example, the dimension of primacy is intertwined with sociality, as primary and secondary rewards (whose reinforcing power is innate or learned, respectively) can be both social (touch and the gesture of thumbs-up) and non-social (food and money). Because primary and secondary rewards show differential neural correlates (Levy & Glimcher, 2011), this could be a confounding dimension for studies focusing on sociality. Further, we suggest ways to account for the multidimensionality of rewards in experimental designs by either incorporating all dimensions as factors, match the rewards on all dimensions, condition rewards with neutral stimuli, or statistically control for dimensions of no interest.

Finally, we discuss the implications of the multidimensionality of rewards in the context of the cued incentive delay task (which was used in Studies 1 and 2) and reward phases. For example, using the same picture of a smiling face as an incentive cue triggering anticipation and as a reward (e.g., Kohls et

al., 2011) may entangle reward phases. Because a smile is a transient and immediate reward (it lasts while it is presented), it is *delivered* both in the beginning and in the end of a trial. This essentially gives two reception phases with the difference of the first being 'passive 'and the other 'active' (which, as shown in Study 3, is also a factor in reward processing).

4.2 Insights for autism research

All the studies in this dissertation covered the topic of autism in relation to reward responsiveness. Studies 1 and 2 directly investigated the modulatory effects of autistic traits (both) and autism (Study 2). In Study 3, an exploratory analysis considered the role of autistic traits on arousal responses to rewarding faces. Finally, in Study 4, we considered the implications of the multidimensionality view on rewards for autism research.

4.2.1 Evaluation of the social motivation theory

According to the social motivation theory, autism is characterised by diminished responsiveness to specifically social rewards. Thus, an interaction of group (autism or higher levels of autistic traits vs. control) and reward domain (social vs. non-social) is expected. Contrary to this theory, we found no interaction of group and reward domain at any processing level (behavioural, neuronal, autonomic) in any of the experiments in this dissertation.

Available research empirically testing the social motivation theory mounts to mixed results reporting both abnormalities and typical processing in autism in each domain (see section 1.3 for an overview). A recent meta-analysis (Clements et al., 2018) reported both hypo- and hyper-activations in the reward network of the autistic brain in response to social and non-social stimuli. The authors propose that these results suggest a general reward impairment and support the social motivation theory in a broader frame, i.e., deficient processing of both social and non-social rewards in autism. However, this conclusion should be re-visited to consider the meaning of reward-related hyper- (instead of the predicted hypo-) activations found in ASC.

Differences between groups, while *atypical* for ASC in comparison to control subjects (Bottini, 2018; Clements et al., 2018; Keifer et al., 2020; Kohls et al., 2012; Neuhaus et al., 2010), should not be automatically equalled to *deficient*. For example, there is no indisputable causality between hypoactivation of a given brain structure and functional deficiency instead of, for example, more

efficient neuronal processing (Scott-Van Zeeland et al., 2010; Shafritz et al., 2015). Hence, to interpret these effects in the light of the social motivation theory, strong evidence directly linking reward-related neuronal atypicalities in ASC with aberrant motivated behaviour, reward learning, or socio-communicative skills (which would suggest functional deficits) is needed. While many studies fail to find such effects (Baumeister et al., 2020; Dichter, Felder, et al., 2012; Greene et al., 2020; Kohls et al., 2013, 2018; Kohls, Thönessen, et al., 2014; Neuhaus et al., 2015; Scott-Van Zeeland et al., 2010), some report symptom severity associated with *reduced* (Barman et al., 2015; Carter Leno et al., 2016; Kohls, Thönessen, et al., 2014) and some (including our data in Studies 1 and 2) with *enhanced* (Dichter, Richey, et al., 2012; van Dongen et al., 2015) neuronal responses. Thus, there is not sufficient evidence to clearly and consistently interpret either direction of group effects (increased or diminished processing in ASC) as functional impairments of social motivation in autism.

On the other hand, social impairments in ASC are evident and core symptoms of this condition (American Psychiatric Association, 2013). While more research is needed to elucidate this, at least two possible interpretations arise. One is that the social motivation theory is challenged in assuming that deficiencies in reward processing *cause* social impairments in autism. It is possible that while reward processing is *different* in this population, the social difficulties result from other mechanisms. For example, it is argued that many individuals on the autism spectrum show typical interests in social relationships (and thus, typical social motivation) and further behavioural manifestations of diminished social motivation in this group (e.g., reduced eye contact) can be explained by other, not pertaining to reward processing, mechanisms, (e.g., a stress reduction strategy; Fennell & Johnson, 2021). Another interpretation is that while there is a true effect of atypical reward processing resulting in social impairments in ASC, the research so far is mixed due to considerable heterogeneity of symptoms in this group, methodological variability in the studies, comorbidities (e.g., social anxiety), other confounding group differences (e.g., face processing), etc. In either case, firm conclusions about the social motivation theory cannot be drawn at this stage. To evaluate it, future research should focus particularly on the relationship between reward processing atypicalities (on multiple levels: neuronal, autonomic, performance) and the social functioning in autism.

4.2.2 Enhanced reward responsiveness in autism and autistic traits

Notably, our data suggest that higher autistic traits and autism are linked to *enhanced* responsiveness to both social and non-social rewards. In the light of the social motivation theory and some previous studies (see section 1.3 for an overview), this result may come as a surprise. However, it is in line with other studies reporting autism being associated with larger ERP amplitudes, hyperactivation in the reward structures, and performance benefits (Cascio et al., 2012; Dichter, Felder, et al., 2012; Dichter, Richey, et al., 2012; Groen et al., 2008; Kohls et al., 2018; Pankert et al., 2014; Sasson et al., 2012; van Dongen et al., 2015; Watson et al., 2015). Importantly, we observed this autism-related enhanced processing in both early reward anticipation and in reception. The first was indexed with an ERP and the latter with pupillary responses, while behavioural performance was comparable for all subjects. This suggests that individuals with autism-like symptoms employ enhanced brain mechanisms, which allow them to achieve similar performance level to those with less or no symptoms.

It is worth noting that we did not observe statistically significant group effects in the late anticipation in either of the two studies. Whereas early anticipation (time-locked to the incentive cues) may be important for establishing the action-reward associations and modulated primarily by *motivation* and *preparation to perform* in order to achieve a particular reward, late anticipation (directly before reward reception) may in contrast involve *expectations* and *preparations to receive and consume* the reward. To our knowledge, we were the first to target anticipatory brain responses across time in relation to autism and autistic traits (but see (Oumeziane et al., 2017) in a neurotypical sample). Therefore, we cannot reject the idea that similar effects were neglected in other studies, which focused solely on the late anticipatory response. Future studies should target both early and late anticipation to provide more evidence before any definite conclusions can be formulated about the role of autistic traits and autism in these two stages.

Notably, although there is accumulating empirical evidence for atypical reward responsiveness in autism, at the same time rewards are prominently utilised in clinical interventions for this group. Appropriate behaviours are promoted in children with ASC by using reinforcement strategies and by pairing naturalistic and external rewards with social situations (Bottini, 2018). Indeed, some of the most popular evidence-based programs use rewards and

reinforcers: the applied behavioural analysis (Foxx, 2008), the pivotal response treatment (Verschuur et al., 2014), and the sociodramatic affective relational intervention (Lerner & Mikami, 2012). If research reporting atypical reward processing in autism is interpreted as impaired reward function in this group, these observations do not align with the treatment programs effectively employing rewards. On the other hand, if enhanced neuronal processing of rewards in ASC and higher levels of autistic traits (as observed in Studies 1 and 2) can be interpreted as higher reward responsiveness (or increased compensatory activation leading to typical behavioural performance), this does not contradict reward-based treatments. Either way, efforts towards an integral interpretation of both empirical and clinical observations should be prioritised in future studies.

Furthermore, it should be noted that our experimental designs incorporated three important aspects which are rarely considered in the literature: controlling for social anxiety traits, familiarity of the social rewards, and employing 'active' rewards. On the one hand, these aspects aimed to eliminate potential confounds in group differences. Controlling for social anxiety traits allowed us to extract autism-specific effects on reward responsiveness and using familiar faces reduced potential group differences in face processing (of course, more comorbidities could and should be controlled for in future studies, e.g., ADHD traits; Kohls, Thönessen, et al., 2014; van Dongen et al., 2015). On the other hand, using 'active' and meaningful (familiar and relevant) social rewards might have boosted the saliency of these stimuli and, in turn, increased their reward value. I discuss this further in the next section.

4.2.3 Saliency of rewards as a key factor

Saliency of rewards can be increased due to internal factors related to motivation and preference. In fact, the social motivation theory proposes that the reward circuit in individuals with ASC is hypoactive for social stimuli, but hyperactive for personal, idiosyncratic, circumscribed interests (Chevallier et al., 2012). Indeed, studies testing this claim support the hypothesised enhanced neuronal responses to pictures of particularly interesting objects for participants on the spectrum (Benning et al., 2016; Cascio et al., 2014; Dichter, Felder, et al., 2012; Kohls et al., 2018; Sasson et al., 2012; Watson et al., 2015). Also, objects related to circumscribed interests have been shown to be more successful reinforcers than social rewards or food (Charlop-Christy & Haymes, 1996). An established neural correlate of saliency detection is the

amygdala (Adolphs, 2010; Gerber et al., 2008) and its altered activation in autism has been repeatedly shown (Baron-Cohen et al., 2000; Dichter, Richey, et al., 2012; Grelotti et al., 2005; Kohls et al., 2013; Nomi & Uddin, 2015). Hence, it has been suggested that the decreased responsiveness of the amygdala to social incentives and enhanced to stimuli related to circumscribed interests in this condition may indicate dysregulation of the reward system through atypical saliency assigned to these categories (Kohls et al., 2012). Therefore, it is interesting to consider whether increasing the saliency of rewards in an external way has the potential to modulate reward processing in autism.

There are several ways in which a stimulus may become more salient. An obvious one is magnitude, e.g., a reward of 1 Euro motivates more than that of 1 Eurocent (Rosell-Negre et al., 2017). This is less clear in social rewards, but it has been attempted, e.g., by using increasingly happy faces as feedback (Spreckelmeyer et al., 2009). Further, Zink and colleagues (Zink et al., 2004) manipulated saliency of monetary rewards by either making them contingent on behaviour or independent of task performance. They observed increased electrodermal and striatal activity for the 'active' money and concluded that the striatum differentiates the saliency of the monetary reward from its nominal value. Note that these results parallel those found in our Study 3, in which the rewarding context (called 'saliency' by Zink and colleagues) increased pupillary and behavioural responses.

Familiarity of rewards, especially social ones (like faces) is another candidate for modulating saliency. Although unfamiliar and novel faces may be more salient to facilitate attention to newly met people (Dubois et al., 1999; Gobbini & Haxby, 2006; Todorov, 2012), familiar faces, especially those personally relevant and laden with emotional meaning, are particularly salient (Bayer et al., 2021; Pierce et al., 2004; Sugiura, 2014). Additionally, familiar faces offering feedback are more interesting (and hence, salient) due to the long-term meaning and significance for future interactions. Therefore, familiar faces of personal relevance and/or importance in a context may be more salient and because of that, more motivating and rewarding.

Together, the saliency and the reward value of the social incentives may be increased by familiarity, relevance, and rewarding context (contingency on behaviour). This reinforces our interpretation that our findings of preserved or even enhanced responses to social rewards in the individuals with autism and higher levels of autistic traits (in comparison to those with low trait levels)

might have been due to the identity of the feedback face: the experimenter. However, Study 1 and 2 did not directly measure the effect of familiarity. Further studies are needed to confirm this interpretation by attempting a replication of our results in an experimental design including a control, non-familiar social reward.

The idea that more salient social rewards are processed without impairments in autism is not solely a descriptive observation, but it is also generates several research questions: 1) can the saliency of social rewards be increased for individuals with autism (for example, by explicitly directing attention towards them)?; 2) how 'much' of social familiarity or personal relevance is necessary to facilitate reward processing in autism?; 3) does saliency of rewards (or lack thereof) explain the mixed results in the literature? Future research should systematically address the role of saliency in reward responsiveness in autism. Ultimately, this may facilitate development of treatment options, which are tailored to an individual.

4.2.4 Reward processing as a transdiagnostic characteristic

Since reward function is also implicated in other psychological conditions (e.g., schizophrenia, addiction, ADHD; Dichter, Damiano, et al., 2012), it is beneficial for the fields of clinical psychology and psychiatry to consider atypicalities in reward responsiveness as a transdiagnostic, rather than ASC-specific, marker. Indeed, a recent systematic review (Aldridge-Waddon et al., 2020) exploring social reward anticipation in psychopathology, found that ADHD, ASC, and schizophrenia spectrum conditions are associated with reduced behavioural anticipation of social rewards, whereas bipolar disorder, eating disorders, and sexual addiction disorders are linked to hyper-anticipation of these rewards. This suggests that atypical social reward anticipation may be a valuable transdiagnostic characteristic with a potential to improve treatment options for autism and other conditions. This is also in line with the Research Domain Criteria (RDoC), a research framework for investigating mental disorders aiming to provide classification schemes based on pathophysiological, rather than clinical, evidence (Insel et al., 2010). RDoC treats mental conditions as brain disorders and characterises dysregulations of brain circuits regardless of diagnostic borders. Thus, a deficit of the reward circuit (manifested in aberrant neuronal indexes) which is shared by different diagnoses can be addressed by a practitioner with the use of the same therapeutic tools.

Furthermore, potential similarities in reward responsiveness within clusters of individuals sharing a diagnostic profile (e.g., common comorbidities or symptoms) open an interesting line of research. Namely, reward responsiveness atypicalities in autism could be address as individual or sub-group characteristics, rather than ASC-specific ones. For example, since ASC and SAD are often co-occurring and they are connected to different profiles of reward processing atypicalities (Richey et al., 2014), one grouping criteria could be the comorbidity of social anxiety. It is possible that this approach can help account for at least some of the inconsistencies in the literature. Additionally, such sub-grouping has the potential to individualise and improve treatment options: A subgroup of ASC individuals with SAD may benefit more than those without the comorbidity from treating social avoidance rather than from promoting social reinforcement (Ouimet et al., 2009). Overall, a continued research effort is needed to provide a thorough and consistent description of the neuronal realisation of the reward function in autism, including comorbidities and subtypes, which could inform the existing and future behavioural intervention approaches.

4.3 Insights for reward research

All four studies in this dissertation addressed and discussed social rewards; three of them comparing their effect to non-social rewards (Studies 1, 2, and 4). Although intuitively we know what rewards are and which ones are social, study designs in empirical research require a careful operationalisation of each phenomenon of interest. Upon a closer look, the concept of a reward becomes elusive: When does a positive stimulus become rewarding? Does it have to be contingent on behaviour? Is *rewarding* the same as *liked* or *pleasant*? Is *rewarding* a property of a stimulus or rather a feature emerging in the interaction of a stimulus and a cognitive agent? In the following, I discuss the insights from this dissertation for the field of reward research.

4.3.1 When is a positive stimulus a reward?

Reward research has been tightly linked to neuroimaging studies of the brain's reward circuit. In such studies, a 'reward' could be anything that elicits activation in its structures. This approach can easily fall victim to the reverse inference fallacy, in which a cognitive process is inferred from a brain activity not directly tested (Poldrack, 2006). However, when talking about social learning and motivation, the meaning of a reward becomes more restricted. In

addition to the stimulus being positive, two more elements are required: contingency on behaviour and context.

Imagine a cashier in a store handing a person the change, smiling, and wishing good day, as they did to all clients before. Should the money or the smile be considered rewarding? I argue that it should not. While the smile and the money are directed towards the receiver and are likely *pleasant* and *liked*, they are not *rewarding*, because the smile is an automatic part of the transaction at a cash register and the money are not *acquired* by the receiver. The receiver did not perform any action without which they would not have received the change or the smile. Similarly, positive feedback from a caregiver reinforces socially appropriate behaviours of a child not only because it is *pleasant* or *liked* by the child, but because the child connects the behaviour to the outcome: Without the action-outcome link, no reward-based learning could occur. Therefore, the reward value of a stimulus is not its feature, but a quality emerging as a result of an action-outcome association and successful performance of this action.

Likewise, watching a movie may be pleasant and may elicit activation in the reward circuit, but it is unlikely that we would consider it *rewarding* for any specific behaviour. On the other hand, one can decide to watch their favourite movie in the evening as a *reward* for working hard during the day. In this case one would *anticipate* this reward throughout the day and would *like* to watch it in the evening. Thus, a positive stimulus (or event) becomes rewarding because of one's own subjective conceptualisation of its meaning in a broader context.

These seemingly trivial observations carry significant value for research. Passively viewed pleasant stimuli in a lab are equivalent to getting the change from a cashier: one *receives* them, but they are not *rewarding* because one did not perform to achieve them. This was tested in Study 3, in which we directly compared arousal responses to the same positive stimuli – smiling faces varying in levels of familiarity and social relevance for participants – in a passive viewing task and in an active task. The results of this study suggest that contingency on behaviour changes the way in which social rewards are processed in comparison to passively viewed stimuli: In the active task, the subjective ratings of rewarding value of the faces were higher, the explained variance in the model was greater, and familiarity of the faces played a role only in this

task. Thus, a positive stimulus is not necessarily a reward, but it can become one depending on a performance of an action and on context.

4.3.2 When is a reward social?

Although there is no clear definition of what makes a reward *social*, there are numerous studies contrasting social and non-social rewards. In Studies 1, 2, and 3, following previous work, we used pictures of smiling faces as social rewards. However, other instances in research include approximations of a human likeness, for example, only a hand (Haffey et al., 2013) or a virtual avatar (Kim et al., 2015). Moreover, research uses also symbolic representations of social feedback known from popular social media, like a Facebook thumbs-up (Oumeziane et al., 2017), or emoticons (Gonzalez-Gadea et al., 2016). Altogether, various stimuli are employed in empirical research to serve as social rewards, which reflects the complexity of this category in real life. But what is it that makes a stimulus a *social reward*?

4.3.2.1 Intended direction

As is the case with other rewards, contingency on behaviour and context are necessary elements also in the social domain. However, as we argued in Study 4, it may be more straightforward to assign a reward value to a non-social stimulus than to a social one. The reason for this is that some social rewards require an additional element in the interplay of the sender, the receiver, and the situation: an intended direction.

Consider an applauded actor in a theatre. Applause is an example of a fundamentally social reward, as the gesture of clapping hands in appreciation of another person's actions is only rewarding due to a social contract: Its value exists because people agree that it means approval and appreciation, not because there is something intrinsically rewarding about seeing or hearing clapping hands. An actor receiving applause after a successful performance in a theatre play finds the clapping hands of the audience rewarding. However, the same stimulus is likely neutral (in terms of reward value) for the spectators and may even elicit negative emotions in a competitive colleague of the applauded performer. Hence, the same stimulus, although generally considered positive, can be perceived as rewarding, neutral, or negative for different individuals sharing the same social situation. The crucial element here is the *intended direction*. The audience intents to reward the actor and not the competitive colleague and they are both aware of this based on the situation. For

this reason, one of them does, and the other one does not find the applause rewarding. This is in line with empirical evidence. For example, reading positive evaluations of one's person is rewarding, while similar evaluations of another person's personality are not (Izuma et al., 2008). Therefore, social stimuli require the element of intended direction to be rewarding.

4.3.3 Conclusion: a definition of a reward

Summing up the considerations detailed above, I propose that a stimulus is a *reward* when it is 1) positive and pleasant, 2) contingent on one's behaviour (a caregiver smiling to a child for their actions), 3) meaningful based on context (watching a movie as a self-planned reward), and, in case of social stimuli, 4) intentionally directed towards the recipient (an applauded actor).

Future research could benefit from considering this definition. Indisputably, operationalisation of this fundamental concept in reward research has the potential to contribute to the comparability of published results and our understanding of reward processing in humans.

4.4 Insights for social neuropsychology research

Natural social situations are dynamic, unpredictable, and immensely complex. These very same characteristics are the core reasons for low experimental control in settings closely resembling natural. Hence, investigating social cognition is an inherently difficult task, as it may be unmanageable to fully grasp the social functioning of humans without immersing them in natural social settings. For example, engagement in *interaction*, which is the primary social situation, is fundamentally different than mere *observation* (Schilbach et al., 2013). Using carefully designed paradigms we – the researchers – aim to extract the cognitive, social, and affective components of the human functioning. For this, we balance experimental control and ecological validity.

In this chapter, I discuss the reasons for and the consequences of the trade-off between ecological validity and experimental control in the research conducted in this dissertation. Further, I critically evaluate the choice to use in pictures of the experimenter as social rewards Studies 1, 2, and 3, with which we aimed to increase the meaningfulness of the social feedback. Finally, I discuss some aspects of my research in the light of the principles of open and reproducible science.

4.4.1 Ecological validity

Ecological validity refers to how well effects observed in a laboratory setting can be generalised to similar situations in natural circumstances. Clearly, ecological validity is important in all endeavours of neuropsychology, including reward research. At least three aspects of experimental stimuli should be considered in the context of the studies in this dissertation: physical vs. digital, static vs. dynamic, and incidental vs. relevant.

4.4.1.1 Physical vs. digital

For the sake of experimental control, researchers usually present the rewards in a digital form, e.g., as visual representations on a computer screen. This was also the case for the stimuli used in Studies 1, 2, and 3. However, rewards which are 'naturally' digital are more ecological in such circumstances than those normally experienced in a physical realm, which is especially vivid in the social domain. For example, a thumbs-up is a symbol existing in the digital space, in which it acquires its meaning (although it is rooted in a physical gesture). Therefore, a symbolic thumbs-up sent by a research assistant sitting in another room (whether factual or not; Oumeziane et al., 2017) is very similar to receiving a symbolic thumbs-up on social media for sharing content. In contrast, a picture of a smiling face of an unfamiliar person shown on a computer screen in a successful trial is not qualitatively close to seeing a friend sitting across a table and dynamically expressing a smile directly in response to one's words. On the other hand, in the times of television, social media, video calls, and other digital means of watching and interacting with others, the digital realm is becoming more and more a part of our natural social domain. Therefore, the digital representations of faces (i.e., 2D pictures presented on a computer screen) we used in Studies 1, 2, and 3 might have been 'real' enough to be ecologically valid.

In the case of the monetary reward in Studies 1 and 2, the digital representations of coins served as a symbol of the real money which subjects received in the end of the study (in line with many other studies; Barman et al., 2015; Baumeister et al., 2020; Delmonte et al., 2012; Greene et al., 2020; Koelewijn et al., 2018; Kohls et al., 2009, 2011, 2013; Kohls, Thönessen, et al., 2014; Scott-Van Zeeland et al., 2010). Although participants were encouraged to imagine they *receive* the money indicated by the symbols when they see them, the pictures of the coins are used rather as an *indication* of the actual monetary rewards

paid later (for more about the distinction between immediate and delayed rewards, see the discussion of temporal proximity in section 3.4.2). Hence, there is a potential to improve this design in future studies by eliminating confounds between social and non-social rewards in terms of temporal proximity. On the other hand, the digitalisation of our everyday life renders non-physical money (e.g., bank transfers, vouchers) as real as coins and banknotes. Therefore, it is important to consider multidimensionality (e.g., temporal proximity) and the consequences of digitalisation of common rewards in future study designs.

4.4.1.2 Static vs. dynamic

A growing number of studies, instead of static pictures, utilise short videos of persons transitioning from a neutral expression to a positive one (Carter Leno et al., 2016; Cox et al., 2015; Dubey et al., 2015, 2017; Kohls et al., 2018; Neuhaus et al., 2015; Sims et al., 2012). This aims to increase the ecological validity of the stimuli, as social signals are dynamic in nature (Dziobek, 2012). Indeed, research suggests that dynamic in comparison to static stimuli are associated with distinct or stronger neuronal activation (Dziobek, 2012; Kilts et al., 2003; LaBar et al., 2003; Perdikis et al., 2017) and higher engagement (Risko et al., 2012).

The stimuli used as rewards in the empirical work of this dissertation were all static and thus lack ecological validity in terms of stimulus dynamics. This limitation, while it leaves room for improvement, was a result of a planned trade-off between ecological validity and experimental control. The primary methods used in Studies 1, 2, and 3 require highly precise timing of the stimulus onset (in the case of the millisecond-resolution of the EEG and ERPs) and rigorous control of the stimuli's luminance (in the case of light-sensitive pupillary responses). These two requirements are difficult to achieve in video stimuli. Thus, while I appreciate and applaud the call for including dynamic stimuli in social neuroscience research, the reasons for this limitation in the current work results from the need to maintain experimental control to ensure high quality of the obtained data. However, it is possible that dynamic (especially social) stimuli, being more natural, would be also considered more rewarding. Therefore, an interesting research question for future studies is whether stimuli dynamics modulate their reward value.

4.4.1.3 Incidental vs. relevant

When one agrees that reward must be coupled with an action and be its consequence (for a discussion, see section 4.3.1), it becomes clear that in everyday life reward and feedback (i.e., response to or evaluation of another person's action) occur simultaneously. For example, a mother smiling to a child for their behaviour offers both positive feedback and a social reward. In experimental settings some rewards are indeed intertwined with feedback, i.e., both are provided in the same stimulus (e.g., Kohls et al., 2011 and our Studies 1, 2, and 3). However, in some studies the rewards are incidental, i.e., are presented in addition to otherwise delivered feedback (e.g., an arbitrary symbol indicating successful performance), either following it (Cox et al., 2015), or occurring simultaneously but without the necessity to be processed (Stavropoulos & Carver, 2014a, 2014b). While they are still contingent on the task performance, the decoupling of feedback and reward may be lacking ecological validity, especially in the case of social incentives.

Further, especially in the social domain, the relevance of the person delivering a reward is of importance. In natural social settings, rewards are typically delivered by familiar persons (partners, friends, colleagues) and those relevant in a given situation (e.g., co-passengers on a train). Therefore, familiarity and contextual relevance, in addition to increasing the reward value of feedback (see section 4.2.3), are also factors boosting ecological validity of experimental stimuli.

In all empirical studies in this dissertation, the reward was delivered simultaneously with feedback, which resembles natural situations. We used pictures of the main experimenter as social rewards (and contrasted them with those of other individuals in Study 3), who was a familiar and relevant person in the given situation. I discuss further the consequences of this rather uncommon research choice (cf. Hayward et al., 2018) in the next section. Together, the stimuli used in the empirical works of this dissertation were relevant in the experimental and social context, which increases the ecological validity of the results.

4.4.2 Experimenter as feedback stimulus

In the context of an empirical study, experimenters are a particular category of social interaction partners. Their faces become familiar during the study preparations, they are relevant to the participants in the context of the

study, and their feedback is especially meaningful in the situation, as they provide information and evaluate performance of the subjects. Moreover, they are likely the only persons who are known by all participants to a similar extend (which balances the level of familiarity and relevance of social reward across the sample). Thus, there is a clear appeal in using experimenters as feedback providers in a study (Hayward et al., 2018).

However, it seems likely that the social relevance of the experimenters depends on how approachable, friendly, and genuine they seem to the participants. Thus, the level of familiarity and relevance may differ between experimenters and studies. A semi-standardised interaction script is required as a part of the experimental procedure to ensure that an experimenter acquires a similar social meaning for all participants. In Studies 1, 2, and 3, such scripts were established and, besides standardised elements like greetings, instructions, and debriefing, also included a small talk to establish a social connection not related directly to the study situation. Experimenters spent a similar amount of time with each participant and had not known them before the visit in the lab. In Study 3, data collection was conducted (and feedback provided) by two experimenters following the same script and no differences between them were found in participants' ratings of their familiarity and relevance or pupillary responses to their pictures (in Studies 1 and 2 there was only one experimenter used as social rewards).

Yet, it can be argued that pictures of such familiar and relevant in the context persons delivered in an experiment are still qualitatively far from natural social feedback. For one, in everyday situations the feedback giver is typically present in the room and offers the evaluation in direct response to one's actions. In an experiment, pictures of smiling faces appear on the screen without an intention of the depicted person to smile in each trial (however, in some studies participants are informed that the feedback is sent in the moment by that person; Oumeziane et al., 2017). Nevertheless, seeing feedback from a person that is important in the situation as an experimenter in a study, likely engages participants on a different level than feedback from absent and unknown people. Moreover, participants are required to continue social exchange with the experimenters after performing in the task, which increases the importance of the latter as immediate interaction partners. Therefore, although there is no direct interaction between participants and experimenters in the moment of the feedback delivery, it is conceivable that processing of this feedback is laden with engagement stemming from the inevitability of further

social interaction. Due to those reasons, I argue that feedback provided by experimenters in our studies was qualitatively different than that which would have been delivered by a picture of a stranger.

This should be considered in the light of the notion that social cognition (including processing of social feedback and reward) is not merely processing of passively acquired information, but rather an active function in which individuals are embedded in and coupled with the perceived world (Thompson, 2010). Indeed, there is a growing body of literature suggesting that cognitive and neuronal processing of social information is fundamentally different in passive observation than in interpersonal interaction (Schilbach et al., 2013). This led to the call for second-person neuroscience, which proposes that interpersonal understanding is based on social interaction and emotional engagement (Schilbach et al., 2013). Thus, social neuroscience should investigate neuronal processing of social information while one interacts with others (second-person approach) and not while one merely observes others (third-person approach). What is more, it has also been suggested that this second- vs. third-person approaches, respectively in natural settings and in laboratories, may explain why some studies fail to reflect typical for autism difficulties in joint attention or attention coordination (Redcay et al., 2013).

To sum up, although not directly tested, it is likely that the familiar face of the experimenter used in Studies 1 and 2 was more rewarding as feedback than a picture of a stranger would have been. Importantly, the social context enclosing the participants and the experimenter included the presence of the latter in the situation, the ongoing need for interaction, and meaningfulness of the experimenter's judgement in the experiment. Certainly, future designs should further improve this by including a truly interactive delivery of the reward and feedback by the experimenter (whether factual, or pre-determined; examples of highly controlled interactive designs in my work can be found elsewhere; Matyjek, Kroczek, et al., 2021; Senderecka et al., 2021). Nevertheless, I argue that the situational context in our studies rendered the participants socially, cognitively, and affectively engaged with the experimenter, which better resembled natural social circumstances.

4.4.3 Estimating the true sizes of effects in social neuropsychology

All analyses reported in this dissertation were conducted within the framework of null hypothesis significance testing. In this framework, a statistical inference is drawn by testing an experimental factor against a null

hypothesis, i.e., that there is no effect (Pernet, 2016). A possible outcome of testing is a negative result: lack of statistically significant effect of a variable of interest on the dependent variable. For example, in this dissertation, against the social motivation theory of autism, we observed no statistically significant interaction effects of group and reward type, and in many cases also no main effects of group. However, a non-significant result does not imply a true negative effect. Another reason for such observation is insufficient power to detect a true small effect. To decide whether a negative result is meaningful and to calculate the size of a sample sufficient to detect an effect with a given power, researchers estimate smallest effect size of interest (SESOI). A SESOI is the smallest difference between groups or conditions that a researcher considers meaningful enough. However, estimating a SESOI is not a trivial task, especially in social neuropsychology.

4.4.3.1 Effect sizes in EEG

The idea of a SESOI is to choose the smallest effect size which could be considered meaningful. For example, when testing whether the average monthly income is meaningfully different for females and males, a researcher could decide that the smallest difference they consider meaningful is 100 Euro. If the difference is smaller than this, the researcher would conclude that there are no significant differences between the genders. However, choosing a SESOI is less straightforward for outcome variables like ERP amplitudes. It is not clear how many μV of a difference should be considered 'meaningful enough'.

A researcher could base their SESOI on previous literature, but the maximum amplitudes vary between ERP components, studies, measurement devices, and participants, and some published studies do not report the unstandardised effect sizes or any effect sizes (e.g., Stavropoulos & Carver, 2014b, 2014a). On the other hand, one could rely on standardised effect sizes, but there is no agreed-upon method of standardising estimates in mixed effects models (used in all studies in this dissertation) due to the complex portioning of variance (Rights & Sterba, 2018). Thus, deciding on a SESOI bears a rather high level of arbitrariness.

4.4.3.2 Publication bias

Another challenge in estimating a SESOI is the presence of a publication bias which is increasing in time and is especially disconcerting in

psychological and clinical fields (Joober et al., 2012). The publication bias entails that, due to a number of complex and systematic mechanisms in academia, positive results are more likely to be published than negative results (Joober et al., 2012). This leads to artificially increased effect sizes and high possibility that the published positive effects are in fact false (Ioannidis, 2005). Thus, a researcher searching for a SESOI in the literature may overestimate it and report an inconclusive negative effect when the effect indeed exists (but is smaller).

It is not clear how problematic publication bias is in the case of reward responsiveness in autism. The only meta-analysis in this topic found no evidence of publication bias, but it included only 13 and only neuroimaging studies (Clements et al., 2018). However, it is evident that the literature on this topic is highly mixed, suggesting low replicability, which co-occurs with publication bias (Joober et al., 2012).

4.4.3.3 Comparability between studies

Finally, due to high complexity of social settings influenced by many situational and both inter- and intrapersonal factors, effect sizes found in social psychology are generally small (Richard et al., 2003) and greatly influenced by a particular study design. For example, while the same paradigm was used in both Studies 1 and 2 in this dissertation (the cued incentive delay task; Knutson et al., 2000), and the magnitudes of social and monetary rewards were similar (the same smiling person and 5 cents in both tasks), we observed consistently larger reward-related responses to money in the first experiment, and to the experimenter's face in the second one. One difference between the experiments was the task the participants performed: In one study participants were asked to *guess* a colour of a card later appearing on a screen, and in another they were asked to perform a reaction time task and had a direct influence on the feedback. Therefore, the task requirements might have substantially influenced responsiveness to social and non-social rewards in these two experiments, and thus, the obtained effect sizes.

This suggests that at least a part of the inconsistencies in the literature of reward processing in autism may be due to a variety of tasks used in these studies (for example, the cued incentive delay task, Richey et al., 2014; the go/no-go task, Kohls et al., 2011; passive viewing, Sepeta et al., 2012; matching tasks, Neuhaus et al., 2015; choice tasks, Watson et al., 2015; etc.). Direct replications of existing results would thus benefit the field. Future research should

address this when drawing conclusions from the existing literature and planning new experiments.

4.4.3.4 Interpreting negative results

To draw conclusions from negative effects (like statistically insignificant group by condition interactions in Study 2), clear evidence for the lack of an effect is needed, including adequate statistical power and additional methods for informing the results. One such method is equivalence testing (e.g., Lakens et al., 2018), in which it is tested whether the obtained effect is at least as large as a pre-defined SESOI. However, because there was no clear way of choosing a SESOI in the studies presented in this dissertation, equivalence testing was not a compelling option.

As an alternative, in Study 2 we calculated Bayes factors to offer relative evidence in favour of either a model with or a model without the interaction term as a predictor (Lakens et al., 2020). Not to disregard any explanatory power of negative results, for the interpretations of the study results we have also considered the overall descriptive pattern of effects. For example, in Study 2 higher levels of autistic traits were consistently linked to increased ERP amplitudes regardless of condition (although this effect reached statistical significance only in early anticipation). Although this cannot be interpreted as a true effect (for the lack of statistical power or absence of true effect), the consistency of results pointing in the predicted direction is a valuable source of information for designing future experiments.

4.4.4 A note on reproducible and open science

The overarching aim of research is to contribute to knowledge. However, when investigating complex, multifaced phenomena, like responsiveness to social and non-social rewards, especially in autism, extensive research is required before conclusions can be made. For this, collaboration of the scientific community is a necessity. A successful realisation of such collaboration needs clear and thorough reporting of previous results, access to the work and data of others, and means to reproduce and replicate previous results. The principles of open and reproducible science allow for these as a conjunction of the key elements in the scientific process (Munafò et al., 2017).

Throughout my doctorate training, I have grown to truly appreciate these principles and to implement many of them in my work. First, all the published

works in this dissertation are available with open access and Study 4 was additionally available as a preprint beforehand. Second, hypotheses, aims, methods, and analyses for Studies 2 and 3 were pre-registered online prior to data collection to facilitate transparency in our research. Third, all the empirical studies presented here have a corresponding online repository including a reproducible analysis script and, where possible, data (Study 3 and, upon submission for publication, Study 2).

Finally, I appreciate science outreach as an important form of engaging the general population in science and working towards inclusiveness of academia. Especially in the context of working with clinical populations, communication of scientific research is the first step to inform interested individuals and to include related stakeholders in future participatory research. For these reasons, in addition to publishing with open access, I have also published lay summaries of all my research projects on the website of our research group.

While there are always more ways to improve the open and reproducible practices in one's work, including the elements described above allowed me to grow as a scholar and to conduct my research in a responsible, future-oriented way. I hope these efforts will contribute in a meaningful way to the ongoing scientific work unravelling reward responsiveness, especially in autism.

4.5 Conclusions

Rewards are crucial elements in our lives which motivate us to engage in actions and reinforce our behaviours. It has been suggested that some symptoms of autism may be caused by deficits in reward processing, but the literature on this topic has so far yielded mixed results. This dissertation investigated social and non-social reward responsiveness with a particular focus on autism and autistic traits. I have presented original data using multiple methodologies (EEG, pupillometry, behavioural measurements) which provided evidence for atypical, but not diminished, processing of both non-social and relevant social rewards in autism and in higher levels of autistic traits. Further, the data presented in this dissertation indicated that familiarity of persons providing social incentives and the rewarding context (whether a reward is contingent on a behaviour) play important roles in reward processing. This empirical work was complemented by a broader theoretical analysis of the multidimensionality of rewards.

The studies in this dissertation have important contributions for the fields of autism, reward, and social neuropsychology research. While autism may be related to atypical processing of rewards, future research should systematically address methodological differences between studies and examine the effect using more salient and ecologically valid stimuli to offer a conclusive interpretation of the available results. The broader field of reward research could benefit from adopting a common definition of reward to achieve more comparable operationalisation across studies. Here, I propose a definition of reward differentiating it from mere positive stimuli, which I based on the empirical and theoretical work conducted in this dissertation. Finally, experimental work in the field of social neuropsychology faces many challenges in the endeavour to increase ecological validity of its results. Therefore, I discussed the ways in which the studies in this dissertation optimised the ecological validity of the obtained results as well as the ways in which this could be even further improved in the future studies. Overall, with this dissertation I hope to contribute to the betterment of our understanding of one of the most fundamental functions of the neurotypical and autistic brain: reward processing.

Abbreviations

Methods and brain structures:

ANS = autonomic nervous system

ASC = autism spectrum condition

ASD = autism spectrum disorder

AQ = autism spectrum quotient (and the score)

CNV = contingent negativity variation

EEG = electroencephalography

ERP = event-related potential

fMRI = functional magnetic resonance imaging

LC-NE = locus coeruleus – norepinephrine

NAcc = nucleus accumbens

OFC = orbitofrontal cortex

RT = reaction time

SPN = stimulus preceding negativity

VTA = ventral tegmental area

VS = ventral striatum

Glossary of terminology

Autism	a neurodevelopmental disorder characterised by social communication and interaction deficits and restricted, repetitive patterns of behaviour
Autistic traits	milder expressions of autism-like symptoms and behaviours
Feedback	response to or evaluation of another person's actions
Reward	outcome of one's motivated behaviour, which is desired and positive, and which is the base for learning and for reinforcing behaviour
Reward domains	social and non-social
Reward phases	anticipation and reception; these phases relate respectively to 'wanting', which is the appetitive motivation towards the reward, and to 'liking', which is the pleasure from receiving the reward
Reward responsiveness	a function of the brain, which defines the degree to which one experiences positive responses to rewards (with the potential to modulate behaviour)
Rewarding context	differentiates between 'active' and 'passive' rewards, i.e., those received in relation to one's actions (contingent on behaviour) and those passively received (regardless of behaviour)
Social cognition	a set of cognitive and affective processes which allow one to understand others and interact with them
Social motivation	a collection of functions and mechanisms encompassing social orientation, social reward, social maintaining
Social motivation theory of autism	a theoretical account proposing that aberrant processing of rewards is the primary deficit in autism, which underlies the social impairments in this condition

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References

Acevedo, B. P., Aron, A., Fisher, H. E., & Brown, L. L. (2012). Neural correlates of long-term intense romantic love. *Social Cognitive and Affective Neuroscience*, *7*(2), 145–159. https://doi.org/10.1093/scan/nsq092

Adolphs, R. (2010). What does the amygdala contribute to social cognition? *Annals of the New York Academy of Sciences*, *1191*(1), 42–61. https://doi.org/10.1111/j.1749-6632.2010.05445.x

Aharon, I., Etcoff, N., Ariely, D., Chabris, C. F., O'Connor, E., & Breiter, H. C. (2001). Beautiful faces have variable reward value: FMRI and behavioral evidence. *Neuron*, *32*(3), 537–551. https://doi.org/10.1016/S0896-6273(01)00491-3

Akaike, H. (1998). Information Theory and an Extension of the Maximum Likelihood Principle. In E. Parzen, K. Tanabe, & G. Kitagawa (Eds.), *Selected Papers of Hirotugu Akaike.* (pp. 199–213). Springer, New York, NY.

Albrecht, K., Abeler, J., Weber, B., & Falk, A. (2014). The brain correlates of the effects of monetary and verbal rewards on intrinsic motivation. *Frontiers in Neuroscience*, *8*, 303. https://doi.org/10.3389/fnins.2014.00303

Aldridge-Waddon, L., Vanova, M., Munneke, J., Puzzo, I., & Kumari, V. (2020). Atypical social reward anticipation as a transdiagnostic characteristic of psychopathology: A meta-analytic review and critical evaluation of current evidence. *Clinical Psychology Review*, *82*, 101942. https://doi.org/10.1016/j.cpr.2020.101942

Allison, C., Baron-Cohen, S., Wheelwright, S., Charman, T., Richler, J., Pasco, G., & Brayne, C. (2008). The Q-CHAT (Quantitative CHecklist for Autism in Toddlers): A Normally Distributed Quantitative Measure of Autistic Traits at 18–24 Months of Age: Preliminary Report. *Journal of*

Autism and Developmental Disorders, *38*(8), 1414–1425. https://doi.org/10.1007/s10803-007-0509-7

American Psychiatric Association. (2013). Diagnostic and statistical manual of mental disorders (5th ed.). In *American Journal of Psychiatry*. https://doi.org/10.1176/appi.books.9780890425596

Antshel, K. M., Zhang-James, Y., Wagner, K. E., Ledesma, A., & Faraone, S. V. (2016). An update on the comorbidity of ADHD and ASD: a focus on clinical management. *Expert Review of Neurotherapeutics*, *16*(3), 279–293. https://doi.org/10.1586/14737175.2016.1146591

Aron, A., Fisher, H., Mashek, D. J., Strong, G., Li, H., & Brown, L. L. (2005). Reward, Motivation, and Emotion Systems Associated With Early-Stage Intense Romantic Love. *Journal of Neurophysiology*, *94*, 327–337. https://doi.org/10.1152/jn.00838.2004

Aston-Jones, G., Rajkowski, J., & Cohen, J. (1999). Role of locus coeruleus in attention and behavioral flexibility. *Biological Psychiatry*, *46*(9), 1309–1320. https://doi.org/10.1016/S0006-3223(99)00140-7

Báez-Mendoza, R., & Schultz, W. (2013). The role of the striatum in social behavior. *Frontiers in Neuroscience*, *7*(233). https://doi.org/10.3389/fnins.2013.00233

Ballard, K., & Knutson, B. (2009). Dissociable neural representations of future reward magnitude and delay during temporal discounting. *NeuroImage*, *45*(1), 143–150. https://doi.org/10.1016/j.neuroimage.2008.11.004

Balodis, I. M., & Potenza, M. N. (2015). Anticipatory Reward Processing in Addicted Populations: A Focus on the Monetary Incentive Delay Task. *Biological Psychiatry*, *77*, 434–444. https://doi.org/10.1016/j.biopsych.2014.08.020

Barman, A., Richter, S., Soch, J., Deibele, A., Richter, A., Assmann, A., Wüstenberg, T., Walter, H., Seidenbecher, C. I., & Schott, B. H. (2015). Gender-specific modulation of neural mechanisms underlying social reward processing by Autism Quotient. *Social Cognitive and Affective Neuroscience*, *10*(11), 1537–1547. https://doi.org/10.1093/scan/nsv044

Baron-Cohen, S., Ring, H. A., Bullmore, E. T., Wheelwright, S., Ashwin, C., & Williams, S. C. R. (2000). The amygdala theory of autism. *Neuroscience & Biobehavioral Reviews*, *24*(3), 355–364. https://doi.org/10.1016/S0149-7634(00)00011-7

Baron-Cohen, S., Wheelwright, S., Hill, J., Raste, Y., & Plumb, I. (2001). The "'Reading the Mind in the Eyes'" Test Revised Version: A Study with Normal Adults, and Adults with Asperger Syndrome or High-functioning Autism. *J. Child Psychol. Psychiat. Association for Child Psychology and Psychiatry*, *42*(2), 241–251. https://doi.org/10.1111/1469-7610.00715

Baron-Cohen, S., Wheelwright, S., Skinner, R., Martin, J., & Clubley, E. (2001). The Autism-Spectrum Quotient (AQ): Evidence from Asperger Syndrome/High-Functioning Autism, Males and Females, Scientists and Mathematicians. *Journal of Autism and Developmental Disorders*, *31*(1), 5–17. https://doi.org/10.1023/A:1005653411471

Bartels, A., & Zeki, S. (2004). The neural correlates of maternal and romantic love. *NeuroImage*, *21*, 1155–1166. https://doi.org/10.1016/j.neuroimage.2003.11.003

Bast, N., Poustka, L., & Freitag, C. M. (2018). The locus coeruleus-norepinephrine system as pacemaker of attention—A developmental mechanism of derailed attentional function in autism spectrum disorder. *The European Journal of Neuroscience*, *47*(2), 115–125. https://doi.org/10.1111/ejn.13795

Baudouin, J.-Y., Gilibert, D., Sansone, S., Tiberghien, G., & Âphane Sansone, S. (2000). When the smile is a cue to familiarity. *Memory*, *8*(5), 285–292. https://doi.org/10.1080/09658210050117717

Bauman, M. L. (2010). Medical comorbidities in autism: Challenges to diagnosis and treatment. *Neurotherapeutics*, *7*(3), 320–327. https://doi.org/10.1016/j.nurt.2010.06.001

Baumeister, S., Moessnang, C., Bast, N., Hohmann, S., Tillmann, J., Goyard, D., Charman, T., Ambrosino, S., Baron-Cohen, S., Beckmann, C., Bölte, S., Bourgeron, T., Rausch, A., Crawley, D., Dell'Acqua, F., Dumas, G., Durston, S., Ecker, C., Floris, D. L., … Group, the A.-2-T. (2020).

Attenuated Anticipation of Social and Monetary Rewards in Autism Spectrum Disorders. *BioRxiv*, 2020.07.06.186650. https://doi.org/10.1101/2020.07.06.186650

Bayer, M., Berhe, O., Dziobek, I., & Johnstone, T. (2021). Rapid Neural Representations of Personally Relevant Faces. *Cerebral Cortex*, *31*(10), 4699–4708. https://doi.org/10.1093/cercor/bhab116

Beck, A., Schlagenhauf, F., Wüstenberg, T., Hein, J., Kienast, T., Kahnt, T., Schmack, K., Hägele, C., Knutson, B., Heinz, A., & Wrase, J. (2009). Ventral Striatal Activation During Reward Anticipation Correlates with Impulsivity in Alcoholics. *Biological Psychiatry*, *66*(8), 734–742.

Bejerot, S., Eriksson, J. M., & Mörtberg, E. (2014). Social anxiety in adult autism spectrum disorder. *Psychiatry Research*, *220*(1–2), 705–707. https://doi.org/10.1016/j.psychres.2014.08.030

Bellini, S. (2006). The Development of Social Anxiety in Adolescents with Autism Spectrum Disorders. *Focus on Autism and Other Developmental Disabilities*, *21*(3), 138–145. https://doi.org/10.1177/10883576060210030201

Benning, S. D., Kovac, M., Campbell, A., Miller, S., Hanna, E. K., Damiano, C. R., Sabatino-DiCriscio, A., Turner-Brown, L., Sasson, N. J., Aaron, R. V., Kinard, J., & Dichter, G. S. (2016). Late Positive Potential ERP Responses to Social and Nonsocial Stimuli in Youth with Autism Spectrum Disorder. *Journal of Autism and Developmental Disorders*, *46*(9), 3068–3077. https://doi.org/10.1007/s10803-016-2845-y

Ben-Shachar, M., Lüdecke, D., & Makowski, D. (2020). effectsize: Estimation of Effect Size Indices and Standardized Parameters. *Journal of Open Source Software*, *5*(56), 2815. https://doi.org/10.21105/joss.02815

Bermudez, M. A., & Schultz, W. (2014). Timing in reward and decision processes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1637), 20120468. https://doi.org/10.1098/rstb.2012.0468

Berridge, K. C. (1996). Food Reward: Brain Substrates of Wanting and Liking. *Neuroscience and Biobehavioral Reviews*, *20*(1), 1–25. https://doi.org/10.1016/0149-7634(95)00033-B

Berridge, K. C. (1999). Pleasure, Pain, Desire, and Dread: Hidden Core Processes of Emotion. In D. Kahneman, E. Diener, & N. Schwarz (Eds.), *Well-Being: The Foundations of Hedonic Psychology* (pp. 527–559). Russell Sage Foundation: New York.

Berridge, K. C. (2009). Wanting and Liking: Observations from the Neuroscience and Psychology Laboratory. *Inquiry*, *52*(4), 378–398. https://doi.org/10.1080/00201740903087359

Berridge, K. C., & Kringelbach, M. L. (2008). Affective neuroscience of pleasure: Reward in humans and animals. *Psychopharmacology*, *199*(3), 457–480. https://doi.org/10.1007/s00213-008-1099-6

Berridge, K. C., & Robinson, T. E. (2016). Liking, wanting, and the incentive-sensitization theory of addiction. *The American Psychologist*, *71*(8), 670–679. https://doi.org/10.1037/amp0000059

Berridge, K. C., Robinson, T. E., & Aldridge, J. W. (2009). Dissecting components of reward: "liking", "wanting", and learning. *Current Opinion in Pharmacology*, *9*(1), 65–73. https://doi.org/10.1016/j.coph.2008.12.014

Bhanji, J. P., & Delgado, M. R. (2014). The social brain and reward: Social information processing in the human striatum. *Wiley Interdisciplinary Reviews: Cognitive Science*, *5*(1). https://doi.org/10.1002/wcs.1266

Bijleveld, E., Custers, R., & Aarts, H. (2009). The Unconscious Eye Opener: Pupil Dilation Reveals Strategic Recruitment of Resources Upon Presentation of Subliminal Reward Cues. *Psychological Science*, *20*(11), 1313–1315. https://doi.org/10.1111/j.1467-9280.2009.02443.x

Bjork, J. M., & Hommer, D. W. (2007). Anticipating instrumentally obtained and passively-received rewards: A factorial fMRI investigation. *Behavioural Brain Research*, *177*(1), 165–170. https://doi.org/10.1016/j.bbr.2006.10.034

Bölte, S., & Poustka, F. (2001). [Factor structure of the Autism Diagnostic Interview-Revised (ADI-R): A study of dimensional versus categorical classification of autistic disorders]. *Zeitschrift fur Kinder- und Jugendpsychiatrie und Psychotherapie*, *29*(3), 221–229. https://doi.org/10.1024//1422-4917.29.3.221

Bottini, S. (2018). Social reward processing in individuals with autism spectrum disorder: A systematic review of the social motivation hypothesis. *Research in Autism Spectrum Disorders*, *45*, 9–26. https://doi.org/10.1016/j.rasd.2017.10.001

Bouret, S., & Richmond, B. J. (2015). Sensitivity of locus ceruleus neurons to reward value for goal-directed actions. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *35*(9), 4005–4014. https://doi.org/10.1523/JNEUROSCI.4553-14.2015

Bowles, S. (2008). Policies Designed for Self-Interested Citizens May Undermine "The Moral Sentiments": Evidence from Economic Experiments. *Science*, *320*(5883), 1605–1609. https://doi.org/10.1126/science.1152110

Bragulat, V., Dzemidzic, M., Bruno, C., Cox, C. A., Talavage, T., Considine, R. V., & Kareken, D. A. (2010). Food-Related Odor Probes of Brain Reward Circuits During Hunger: A Pilot fMRI Study. *Obesity*, *18*(8), 1566–1571. https://doi.org/10.1038/oby.2010.57

Brisson, J., Mainville, M., Mailloux, D., Beaulieu, C., Serres, J., & Sirois, S. (2013). Pupil diameter measurement errors as a function of gaze direction in corneal reflection eyetrackers. *Behavior Research Methods*, *45*(4), 1322–1331. https://doi.org/10.3758/s13428-013-0327-0

Broyd, S. J., Richards, H. J., Helps, S. K., Chronaki, G., Bamford, S., & Sonuga-Barke, E. J. S. (2012). An electrophysiological Monetary Incentive Delay (e-MID) task: A way to decompose the different components of neural response to positive and negative monetary reinforcement. *Journal of Neuroscience Methods*, *209*(1), 40–49. https://doi.org/10.1016/j.jneumeth.2012.05.015

Brunia, C. H. M., van Boxtel, G. J. M., & Böcker, K. B. E. (2012). Negative Slow Waves as Indices of Anticipation: The Bereitschaftspotential, the Contingent Negative Variation, and the Stimulus-Preceding Negativity. In *The Oxford Handbook of Event-Related Potential Components*.

Buss, A. H. (1983). Social rewards and personality. *Journal of Personality and Social Psychology*, *44*(3), 553–563. https://doi.org/10.1037/0022-3514.44.3.553

Caharel, S., Courtay, N., Bernard, C., Lalonde, R., & Rebaï, M. (2005). Familiarity and emotional expression infuence an early stage of face processing: An electrophysiological study. *Brain and Cognition*, *59*, 96–100. https://doi.org/10.1016/j.bandc.2005.05.005

Carsten, T., Kostandyan, M., Boehler, C. N., & Krebs, R. M. (2021). Comparing the motivational value of rewards and losses in an EEG-pupillometry study. *European Journal of Neuroscience*, *53*(6), 1822–1838. https://doi.org/10.1111/ejn.15064

Carter Leno, V., Naples, A., Cox, A., Rutherford, H., & Mcpartland, J. C. (2016). Common and distinct modulation of electrophysiological indices of feedback processing by autistic and psychopathic traits. *Social Neuroscience*, *11*(4), 455–466. https://doi.org/10.1080/17470919.2015.1108223

Carter, R. M., Bowling, D. L., Reeck, C., & Huettel, S. A. (2012). A Distinct Role of the Temporal-Parietal Junction in Predicting Socially Guided Decisions. *Science*, *337*(6090), 109–111. https://doi.org/10.1126/science.1219681

Carver, C. S., & White, T. L. (1994). Behavioral inhibition, behavioral activation, and affective responses to impending reward and punishment: The BIS/BAS Scales. *Journal of Personality and Social Psychology*, *67*(2), 319–333.

Cascio, C. J., Foss-Feig, J. H., Heacock, J. L., Newsom, C. R., Cowan, R. L., Benningfield, M. M., Rogers, B. P., & Cao, A. (2012). Response of neural reward regions to food cues in autism spectrum disorders. *Journal of Neurodevelopmental Disorders*, *4*(9). https://doi.org/10.1186/1866-1955-4-9

Cascio, C. J., Foss-Feig, J. H., Heacock, J., Schauder, K. B., Loring, W. A., Rogers, B. P., Pryweller, J. R., Newsom, C. R., Cockhren, J., Cao, A., & Bolton, S. (2014). Affective neural response to restricted interests in autism spectrum disorders. *Journal of Child Psychology and Psychiatry and Allied Disciplines*, *55*(2), 162–171. https://doi.org/10.1111/jcpp.12147

Cash-Padgett, T., Azab, H., Yoo, S. B. M., & Hayden, B. Y. (2018). Opposing pupil responses to offered and anticipated reward values. *Animal Cognition*, *21*(5), 671–684. https://doi.org/10.1007/s10071-018-1202-2

Chae, Y., Lee, J.-C., Park, K.-M., Kang, O.-S., Park, H.-J., & Lee, H. (2008). Subjective and Autonomic Responses to Smoking-Related Visual Cues. *The Journal of Physiological Sciences*, *58*(2), 139–145. https://doi.org/10.2170/physiolsci.RP014207

Chakrabarti, S., & Fombonne, E. (2005). Pervasive Developmental Disorders in Preschool Children: Confirmation of High Prevalence. *American Journal of Psychiatry*, *162*(6), 1133–1141. https://doi.org/10.1176/appi.ajp.162.6.1133

Charlop-Christy, M. H., & Haymes, L. K. (1996). Using obsessions as reinforcers with and without mild reductive procedures to decrease inappropriate behaviors of children with autism. *Journal of Autism and Developmental Disorders*, *26*(5), 527–546. https://doi.org/10.1007/BF02172274

Chevallier, C., Kohls, G., Troiani, V., Brodkin, E. S., & Schultz, R. T. (2012). The social motivation theory of autism. *Trends in Cognitive Sciences*, *16*(4), 231–239. https://doi.org/10.1016/j.tics.2012.02.007

Chiarotti, F., & Venerosi, A. (2020). Epidemiology of Autism Spectrum Disorders: A Review of Worldwide Prevalence Estimates Since 2014. *Brain Sciences*, *10*(5), 274. https://doi.org/10.3390/brainsci10050274

Chib, V. S., Rangel, A., Shimojo, S., & O'Doherty, J. P. (2009). Evidence for a Common Representation of Decision Values for Dissimilar Goods in Human Ventromedial Prefrontal Cortex. *Journal of Neuroscience*, *29*(39), 12315–12320. https://doi.org/10.1523/JNEUROSCI.2575-09.2009

Clements, C. C., Zoltowski, A. R., Yankowitz, L. D., Yerys, B. E., Schultz, R. T., & Herrington, J. D. (2018). Evaluation of the Social Motivation Hypothesis of Autism. *JAMA Psychiatry*, *75*(8), 797. https://doi.org/10.1001/jamapsychiatry.2018.1100

Constantino, J. N., & Gruber, C. P. (2005). *The Social Responsiveness Scale: SRS-2*. Western Psychological Services.

Constantino, J. N., & Todd, R. D. (2003). Autistic Traits in the General Population: A Twin Study. *Archives of General Psychiatry*, *60*(5), 524–530. https://doi.org/10.1001/archpsyc.60.5.524

Cox, A., Kohls, G., Naples, A. J., Mukerji, C. E., Coffman, M. C., Rutherford, H. J. V., Mayes, L. C., & Mcpartland, J. C. (2015). Diminished social reward anticipation in the broad autism phenotype as revealed by event-related brain potentials. *Social Cognitive and Affective Neuroscience*, *10*, 1357–1364. https://doi.org/10.1093/scan/nsv024

Cremers, H. R., Veer, I. M., Spinhoven, P., Rombouts, S. A. R. B., & Roelofs, K. (2015). Neural sensitivity to social reward and punishment anticipation in social anxiety disorder. *Frontiers in Behavioral Neuroscience*, *8*(439), 1–9. https://doi.org/10.3389/fnbeh.2014.00439

Damiano, C. R., Cockrell, D. C., Dunlap, K., Hanna, E. K., Miller, S., Bizzell, J., Kovac, M., Turner-Brown, L., Sideris, J., Kinard, J., & Dichter, G. S. (2015). Neural mechanisms of negative reinforcement in children and adolescents with autism spectrum disorders. *Journal of Neurodevelopmental Disorders*, *7*(1), 12. https://doi.org/10.1186/s11689-015-9107-8

Davidson, M. (2017). Vaccination as a cause of autism—Myths and controversies. *Dialogues in Clinical Neuroscience*, *19*(4), 403–407. https://doi.org/10.31887/DCNS.2017.19.4/mdavidson

Dawson, G., Carver, L., Meltzoff, A. N., Panagiotides, H., McPartland, J., & Webb, S. J. (2002). Neural Correlates of Face and Object Recognition in Young Children with Autism Spectrum Disorder, Developmental Delay, and Typical Development. *Child Development*, *73*(3), 700–717. https://doi.org/10.1111/1467-8624.00433

Dawson, G., Meltzoff, A. N., Osterling, J., & Rinaldi, J. (1998). Neuropsychological correlates of early symptoms of autism. *Child Development*, *69*(5), 1276–1285.

Dawson, G., Osterling, J., Rinaldi, J., Carver, L., & McPartland, J. (2001). Brief Report: Recognition Memory and Stimulus-Reward Associations: Indirect Support for the Role of Ventromedial Prefrontal Dysfunction in Autism. *Journal of Autism and Developmental Disorders*, *31*(3), 337–341. https://doi.org/10.1023/A:1010751404865

Dawson, G., Webb, S. J., & McPartland, J. (2005). Understanding the Nature of Face Processing Impairment in Autism: Insights From Behavioral and Electrophysiological Studies. *Developmental Neuropsychology*, *27*(3), 403–424. https://doi.org/10.1207/s15326942dn2703_6

Dawson, G., Webb, S. J., Wijsman, E., Schellenberg, G., Estes, A., Munson, J., & Faja, S. (2005). Neurocognitive and electrophysiological evidence of altered face processing in parents of children with autism: Implications for a model of abnormal development of social brain circuitry in autism. *Development and Psychopathology*, *17*, 679–697. https://doi.org/10.1017/S0954579405050327

Deaner, R. O., Shepherd, S. V., & Platt, M. L. (2007). Familiarity accentuates gaze cuing in women but not men. *Biology Letters*, *3*(1), 65–68. https://doi.org/10.1098/rsbl.2006.0564

Deci, E. L. (1971). Effects of externally mediated rewards on intrinsic motivation. *Journal of Personality and Social Psychology*, *18*(1), 105–115. https://doi.org/10.1037/h0030644

Deci, E. L., Koestner, R., & Ryan, R. M. (1999). A Meta-Analytic Review of Experiments Examining the Effects of Extrinsic Rewards on Intrinsic Motivation. *Psychological Bulletin*, *125*(6), 627–633.

Deci, E. L., Koestner, R., & Ryan, R. M. (2001). Extrinsic Rewards and Intrinsic Motivation in Education: Reconsidered Once Again. *Review of Educational Research*, *71*(1), 1–27. https://doi.org/10.3102/00346543071001001

Delgado, M. R., Labouliere, C. D., & Phelps, E. A. (2006). Fear of losing money? Aversive conditioning with secondary reinforcers. *Social Cognitive and Affective Neuroscience*, *1*(3), 250–259. https://doi.org/10.1093/scan/nsl025

Delmonte, S., Balsters, J. H., McGrath, J., Fitzgerald, J., Brennan, S., Fagan, A. J., & Gallagher, L. (2012). Social and monetary reward processing in autism spectrum disorders. *Molecular Autism*, *3*(1), 7. https://doi.org/10.1186/2040-2392-3-7

Demurie, E., Roeyers, H., Baeyens, D., & Sonuga-Barke, E. (2011). Common alterations in sensitivity to type but not amount of reward in ADHD and autism spectrum disorders. *Journal of Child Psychology and Psychiatry and Allied Disciplines*, *52*(11), 1164–1173. https://doi.org/10.1111/j.1469-7610.2010.02374.x

Demurie, E., Roeyers, H., Baeyens, D., & Sonuga-Barke, E. (2013). Domain-general and domain-specific aspects of temporal discounting in children with ADHD and autism spectrum disorders (ASD): A proof of concept study. *Research in Developmental Disabilities*, *34*(6), 1870–1880. https://doi.org/10.1016/j.ridd.2013.03.011

Demurie, E., Roeyers, H., Wiersema, J. R., & Sonuga-Barke, E. (2016). No Evidence for Inhibitory Deficits or Altered Reward Processing in ADHD: Data From a New Integrated Monetary Incentive Delay Go/No-Go Task. *Journal of Attention Disorders*, *20*(4), 353–367. https://doi.org/10.1177/1087054712473179

Dichter, G. S., & Adolphs, R. (2012). Reward processing in autism: A thematic series. *Journal of Neurodevelopmental Disorders*, *4*(20). https://doi.org/doi.org/10.1186/1866-1955-4-20

Dichter, G. S., Damiano, C. A., & Allen, J. A. (2012). Reward circuitry dysfunction in psychiatric and neurodevelopmental disorders and genetic syndromes: Animal models and clinical findings. *Journal of Neurodevelopmental Disorders*, *4*(19). https://doi.org/10.1186/1866-1955-4-19

Dichter, G. S., Felder, J. N., Green, S. R., Rittenberg, A. M., Sasson, N. J., & Bodfish, J. W. (2012). Reward circuitry function in autism spectrum disorders. *Social Cognitive and Affective Neuroscience*, *7*(2), 160–172. https://doi.org/10.1093/scan/nsq095

Dichter, G. S., Richey, J. A., Rittenberg, A. M., Sabatino, A., & Bodfish, J. W. (2012). Reward Circuitry Function in Autism During Face Anticipation and Outcomes. *Journal of Autism and Developmental Disorders*, *42*, 147–160. https://doi.org/10.1007/s10803-011-1221-1

Diekhof, E. K., Kaps, L., Falkai, P., & Gruber, O. (2012). The role of the human ventral striatum and the medial orbitofrontal cortex in the representation of reward magnitude – An activation likelihood

estimation meta-analysis of neuroimaging studies of passive reward expectancy and outcome processing. *Neuropsychologia*, *50*(7), 1252–1266. https://doi.org/10.1016/j.neuropsychologia.2012.02.007

Dobel, C., Geiger, L., Bruchmann, M., Putsche, C., Schweinberger, S. R., & Junghöfer, M. (2008). On the interplay between familiarity and emotional expression in face perception. *Psychological Research*, *72*, 580–586. https://doi.org/10.1007/s00426-007-0132-4

Dobs, K., Isik, L., Pantazis, D., & Kanwisher, N. (2019). How face perception unfolds over time. *Nature Communications*, *10*(1), 1258. https://doi.org/10.1038/s41467-019-09239-1

Drimalla, H., Landwehr, N., Baskow, I., Behnia, B., Roepke, S., Dziobek, I., & Scheffer, T. (2019). Detecting Autism by Analyzing a Simulated Social Interaction. In M. Berlingerio, F. Bonchi, T. Gärtner, N. Hurley, & G. Ifrim (Eds.), *Machine Learning and Knowledge Discovery in Databases* (pp. 193–208). Springer International Publishing. https://doi.org/10.1007/978-3-030-10925-7_12

Dubey, I., Ropar, D., & de C Hamilton, A. F. (2015). Measuring the value of social engagement in adults with and without autism. *Molecular Autism*, *6*(1), 35. https://doi.org/10.1186/s13229-015-0031-2

Dubey, I., Ropar, D., & de C. Hamilton, A. F. (2017). Brief Report: A Comparison of the Preference for Viewing Social and Non-social Movies in Typical and Autistic Adolescents. *Journal of Autism and Developmental Disorders*, *47*, 514–519. https://doi.org/10.1007/s10803-016-2974-3

Dubois, S., Rossion, B., Schiltz, C., Bodart, J. M., Michel, C., Bruyer, R., & Crommelinck, M. (1999). Effect of Familiarity on the Processing of Human Faces. *NeuroImage*, *9*(3), 278–289. https://doi.org/10.1006/nimg.1998.0409

Dziobek, I. (2012). Towards a More Ecologically Valid Assessment of Empathy. *Emotion Review*, *4*(1), 18–19. https://doi.org/10.1177/1754073911421390

Dziobek, I., Bahnemann, M., Convit, A., & Heekeren, H. R. (2010). The Role of the Fusiform-Amygdala System in the Pathophysiology of Autism.

Archives of General Psychiatry, *67*(4), 397–405. https://doi.org/10.1001/archgenpsychiatry.2010.31

English, M. C. W., Gignac, G. E., Visser, T. A. W., Whitehouse, A. J. O., Enns, J. T., & Maybery, M. T. (2021). The Comprehensive Autistic Trait Inventory (CATI): Development and validation of a new measure of autistic traits in the general population. *Molecular Autism*, *12*(1), 37. https://doi.org/10.1186/s13229-021-00445-7

Ethridge, P., Kujawa, A., Dirks, M. A., Arfer, K. B., Kessel, E. M., Klein, D. N., & Weinberg, A. (2017). Neural responses to social and monetary reward in early adolescence and emerging adulthood. *Psychophysiology*, *54*(12), 1786–1799. https://doi.org/10.1111/psyp.12957

Ewing, L., Pellicano, E., & Rhodes, G. (2013). Using Effort to Measure Reward Value of Faces in Children with Autism. *PLOS ONE*, *8*(11), e79493. https://doi.org/10.1371/journal.pone.0079493

Farroni, T., Menon, E., Rigato, S., & Johnson, M. H. (2007). The perception of facial expressions in newborns. *European Journal of Developmental Psychology*, *4*(1), 2–13. https://doi.org/10.1080/17405620601046832

Faul, F., Erdfelder, E., Buchner, A., & Lang, A.-G. (2009). Statistical power analyses using G*Power 3.1: Tests for correlation and regression analyses. *Behavior Research Methods*, *41*(4), 1149–1160.

Faul, F., Erdfelder, E., Lang, A.-G., & 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. https://doi.org/10.3758/BF03193146

Fennell, L. C. P., & Johnson, S. A. (2021). Examination of professional biases about autism: How can we do better? *The Clinical Neuropsychologist*, *0*(0), 1–22. https://doi.org/10.1080/13854046.2021.1958922

Fletcher-Watson, S., Findlay, J. M., Leekam, S. R., & Benson, V. (2008). Rapid Detection of Person Information in a Naturalistic Scene. *Perception*, *37*(4), 571–583. https://doi.org/10.1068/p5705

Foulkes, L., Bird, G., Gökçen, E., McCrory, E., & Viding, E. (2015). Common and distinct impacts of autistic traits and alexithymia on social

reward. *PLoS ONE*, *10*(4), e0121018. https://doi.org/10.1371/journal.pone.0121018

Foxx, R. M. (2008). Applied Behavior Analysis Treatment of Autism: The State of the Art. *Child and Adolescent Psychiatric Clinics of North America*, *17*(4), 821–834. https://doi.org/10.1016/j.chc.2008.06.007

Galbin, A. (2014). An introduction to social constructionism. *Social Research Reports*, *6*(26), 82–92.

Garretson, H. B., Fein, D., & Waterhouse, L. (1990). Sustained attention in children with autism. *Journal of Autism and Developmental Disorders*, *20*(1), 101–114. https://doi.org/10.1007/BF02206860

Gerber, A. J., Posner, J., Gorman, D., Colibazzi, T., Yu, S., Wang, Z., Kangarlu, A., Zhu, H., Russell, J., & Peterson, B. S. (2008). An affective circumplex model of neural systems subserving valence, arousal, and cognitive overlay during the appraisal of emotional faces. *Neuropsychologia*, *46*(8), 2129–2139. https://doi.org/10.1016/j.neuropsychologia.2008.02.032

Geurts, H. M., Luman, M., & Meel, C. S. V. (2008). What's in a game: The effect of social motivation on interference control in boys with ADHD and autism spectrum disorders. *Journal of Child Psychology and Psychiatry*, *49*(8), 848–857. https://doi.org/10.1111/j.1469-7610.2008.01916.x

Gilbertson, L., Lutfi, R. A., & Weismer, S. E. (2017). Auditory Preference of Children with Autism Spectrum Disorders. *Cognitive Processing*, *18*(2), 205–209. https://doi.org/10.1007/s10339-016-0787-0

Glimcher, P. W., & Rustichini, A. (2004). Neuroeconomics: The Consilience of Brain and Decision. *Science*, *306*(5695), 447–452. https://doi.org/10.1126/science.1102566

Gobbini, M. I., Gors, J. D., Halchenko, Y. O., Rogers, C., Guntupalli, J. S., Hughes, H., & Cipolli, C. (2013). Prioritized Detection of Personally Familiar Faces. *PLoS ONE*, *8*(6), e66620. https://doi.org/10.1371/journal.pone.0066620

Gobbini, M. I., & Haxby, J. V. (2006). Neural response to the visual familiarity of faces. *Brain Research Bulletin*, *71*(1), 76–82. https://doi.org/10.1016/j.brainresbull.2006.08.003

Gobbini, M. I., & Haxby, J. V. (2007). Neural systems for recognition of familiar faces. *Neuropsychologia*, *45*(1), 32–41. https://doi.org/10.1016/j.neuropsychologia.2006.04.015

Goldstein, R. Z., Cottone, L. A., Jia, Z., Maloney, T., Volkow, N. D., & Squires, N. K. (2006). The effect of graded monetary reward on cognitive event-related potentials and behavior in young healthy adults. *International Journal of Psychophysiology*, *62*(2), 272–279. https://doi.org/doi.org/10.1016/j.ijpsycho.2006.05.006

Gonzalez-Gadea, M. L., Sigman, M., Rattazzi, A., Lavin, C., Rivera-Rei, A., Marino, J., Manes, F., & Ibanez, A. (2016). Neural markers of social and monetary rewards in children with Attention-Deficit/Hyperactivity Disorder and Autism Spectrum Disorder. *Scientific Reports*, *6*, 30588. https://doi.org/10.1038/srep30588

Greene, R. K., Damiano-Goodwin, C. R., Walsh, E., Bizzell, J., & Dichter, G. S. (2020). Neural Mechanisms of Vicarious Reward Processing in Adults with Autism Spectrum Disorder. *Autism Research and Treatment*, *2020*, e8014248. https://doi.org/10.1155/2020/8014248

Grelotti, D. J., Gauthier, I., & Schultz, R. T. (2002). Social interest and the development of cortical face specialization: What autism teaches us about face processing. *Developmental Psychobiology*, *40*(3), 213–225. https://doi.org/10.1002/dev.10028

Grelotti, D. J., Klin, A. J., Gauthier, I., Skudlarski, P., Cohen, D. J., Gore, J. C., Volkmar, F. R., & Schultz, R. T. (2005). FMRI activation of the fusiform gyrus and amygdala to cartoon characters but not to faces in a boy with autism. *Neuropsychologia*, *43*(3), 373–385. https://doi.org/10.1016/j.neuropsychologia.2004.06.015

Grey Walter, W., Cooper, R., Aldridge, V. J., McCallum, W. C., & Winter, A. L. (1964). Contingent Negative Variation: An Electric Sign of Sensorimotor Association and Expectancy in the Human Brain. *Nature*, *203*, 380–384.

Groen, Y., Wijers, A. A., Mulder, L. J. M., Waggeveld, B., Minderaa, R. B., & Althaus, M. (2008). Error and feedback processing in children with ADHD and children with Autistic Spectrum Disorder: An EEG event-related potential study. *Clinical Neurophysiology*, *119*, 2476–2493. https://doi.org/10.1016/j.clinph.2008.08.004

Gu, R., Huang, W., Camilleri, J., Xu, P., Wei, P., Eickhoff, S. B., & Feng, C. (2019). Love is analogous to money in human brain: Coordinate-based and functional connectivity meta-analyses of social and monetary reward anticipation. *Neuroscience & Biobehavioral Reviews*, *100*, 108–128. https://doi.org/10.1016/j.neubiorev.2019.02.017

Guitart-Masip, M., Bunzeck, N., Stephan, K. E., Dolan, R. J., & Düzel, E. (2010). Contextual Novelty Changes Reward Representations in the Striatum. *Journal of Neuroscience*, *30*(5), 1721–1726. https://doi.org/10.1523/JNEUROSCI.5331-09.2010

Haber, S. N., & Knutson, B. (2010). The Reward Circuit: Linking Primate Anatomy and Human Imaging. *Neuropsychopharmacology*, *35*(1), 4–26. https://doi.org/10.1038/npp.2009.129

Haffey, A., Press, C., O'Connell, G., & Chakrabarti, B. (2013). Autistic Traits Modulate Mimicry of Social but not Nonsocial Rewards. *Autism Research*, *6*(6), 614–620. https://doi.org/10.1002/aur.1323

Hasson, U., Nir, Y., Levy, I., Fuhrmann, G., & Malach, R. (2004). Intersubject Synchronization of Cortical Activity During Natural Vision. *Science*, *303*(5664), 1634–1640. https://doi.org/10.1126/science.1089506

Haxby, J. V., Gobbini, M. I., Furey, M. L., Ishai, A., Schouten, J. L., & Pietrini, P. (2001). Distributed and Overlapping Representations of Faces and Objects in Ventral Temporal Cortex. *Science*, *293*(5539), 2425–2430. https://doi.org/10.1126/science.1063736

Hayward, D. A., Pereira, E. J., Otto, A. R., & Ristic, J. (2018). Smile! Social reward drives attention. *Journal of Experimental Psychology: Human Perception and Performance*, *44*(2), 206–214. https://doi.org/10.1037/xhp0000459

Held-Poschardt, D., Sterzer, P., Schlagenhauf, F., Pehrs, C., Wittmann, A., Stoy, M., Hägele, C., Knutson, B., Heinz, A., & Ströhle, A. (2018). Reward and loss anticipation in panic disorder: An fMRI study. *Psychiatry Research. Neuroimaging*, *271*, 111–117. https://doi.org/10.1016/j.pscychresns.2017.11.005

Hoekstra, R. A., Bartels, M., Verweij, C. J. H., & Boomsma, D. I. (2007). Heritability of Autistic Traits in the General Population. *Archives of Pediatrics & Adolescent Medicine*, *161*(4), 372. https://doi.org/10.1001/archpedi.161.4.372

Hofmeister, J., & Sterpenich, V. (2015). A Role for the Locus Ceruleus in Reward Processing: Encoding Behavioral Energy Required for Goal-Directed Actions. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *35*(29), 10387–10389. https://doi.org/10.1523/JNEUROSCI.1734-15.2015

Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal: Journal of Mathematical Methods in Biosciences*, *50*(3), 346–363. https://doi.org/10.1002/bimj.200810425

Hudenko, W. J., Stone, W., & Bachorowski, J.-A. (2009). Laughter Differs in Children with Autism: An Acoustic Analysis of Laughs Produced by Children With and Without the Disorder. *Journal of Autism and Developmental Disorders*, *39*(10), 1392–1400. https://doi.org/10.1007/s10803-009-0752-1

Hulst, B. M. van, Zeeuw, P. de, Bos, D. J., Rijks, Y., Neggers, S. F. W., & Durston, S. (2017). Children with ADHD symptoms show decreased activity in ventral striatum during the anticipation of reward, irrespective of ADHD diagnosis. *Journal of Child Psychology and Psychiatry*, *58*(2), 206–214. https://doi.org/10.1111/jcpp.12643

Hurley, R. S. E., Losh, M., Parlier, M., Reznick, J. S., & Piven, J. (2007). The Broad Autism Phenotype Questionnaire. *Journal of Autism and Developmental Disorders*, *37*(9), 1679–1690. https://doi.org/10.1007/s10803-006-0299-3

Hyman, S. E. (2007). Can neuroscience be integrated into the DSM-V? *Nature Reviews Neuroscience*, *8*(9), 725–732. https://doi.org/10.1038/nrn2218

Insel, T., Cuthbert, B., Garvey, M., Heinssen, R., Pine, D. S., Quinn, K., Sanislow, C., & Wang, P. (2010). Research Domain Criteria (RDoC): Toward a New Classification Framework for Research on Mental Disorders. *American Journal of Psychiatry*, *167*(7), 748–751. https://doi.org/10.1176/appi.ajp.2010.09091379

Ioannidis, J. P. A. (2005). Why Most Published Research Findings Are False. *PLoS Medicine*, *2*(8), e124. https://doi.org/10.1371/journal.pmed.0020124

Izuma, K., Saito, D. N., & Sadato, N. (2008). Processing of Social and Monetary Rewards in the Human Striatum. *Neuron*, *58*, 284–294. https://doi.org/10.1016/j.neuron.2008.03.020

Jiang, T., Soussignan, R., Schaal, B., & Royet, J.-P. (2015). Reward for food odors: An fMRI study of liking and wanting as a function of metabolic state and BMI. *Social Cognitive and Affective Neuroscience*, *10*(4), 561–568. https://doi.org/10.1093/scan/nsu086

Joober, R., Schmitz, N., Annable, L., & Boksa, P. (2012). Publication bias: What are the challenges and can they be overcome? *Journal of Psychiatry & Neuroscience : JPN*, *37*(3), 149–152. https://doi.org/10.1503/jpn.120065

Joshi, S., Li, Y., Kalwani, R. M., & Gold, J. I. (2016). Relationships between Pupil Diameter and Neuronal Activity in the Locus Coeruleus, Colliculi, and Cingulate Cortex. *Neuron*, *89*(1), 221–234. https://doi.org/10.1016/J.NEURON.2015.11.028

Juechems, K., Balaguer, J., Ruz, M., & Summerfield, C. (2017). Ventromedial Prefrontal Cortex Encodes a Latent Estimate of Cumulative Reward. *Neuron*, *93*(3), 705-714.e4. https://doi.org/10.1016/j.neuron.2016.12.038

Kable, J. W., & Glimcher, P. W. (2007). The neural correlates of subjective value during intertemporal choice. *Nature Neuroscience*, *10*(12), 1625–1633. https://doi.org/10.1038/nn2007

Kanner, L. (1943). Autistic disturbances of affective contact. *Nervous Child*, *2*(3), 217–250.

Kappenman, E. S., & Luck, S. J. (2012). The Oxford Handbook of Event-Related Potential Components. In *The Oxford Handbook of Event-Related Potential Components*. https://doi.org/10.1093/oxfordhb/9780195374148.001.0001

Kass, R. E., & Raftery, A. E. (1995). Bayes Factors. *Journal of the American Statistical Association*, *90*(430), 773–795. https://doi.org/10.1080/01621459.1995.10476572

Kätsyri, J., de Gelder, B., & de Borst, A. W. (2020). Amygdala responds to direct gaze in real but not in computer-generated faces. *NeuroImage*, *204*, 116216. https://doi.org/10.1016/j.neuroimage.2019.116216

Keifer, C. M., Day, T. C., Hauschild, K. M., & Lerner, M. D. (2021). Social and Nonsocial Reward Anticipation in Typical Development and Autism Spectrum Disorders: Current Status and Future Directions. *Current Psychiatry Reports*, *23*(6), 32. https://doi.org/10.1007/s11920-021-01247-7

Keifer, C. M., Mikami, A. Y., Morris, J. P., Libsack, E. J., & Lerner, M. D. (2020). Prediction of social behavior in autism spectrum disorders: Explicit versus implicit social cognition. *Autism*, *24*(7), 1758–1772. https://doi.org/10.1177/1362361320922058

Kilts, C. D., Egan, G., Gideon, D. A., Ely, T. D., & Hoffman, J. M. (2003). Dissociable neural pathways are involved in the recognition of emotion in static and dynamic facial expressions. *NeuroImage*, *18*(1), 156–168. https://doi.org/10.1006/nimg.2002.1323

Kim, H., Shimojo, S., & O'Doherty, J. P. (2011). Overlapping Responses for the Expectation of Juice and Money Rewards in Human Ventromedial Prefrontal Cortex. *Cerebral Cortex*, *21*(4), 769–776. https://doi.org/10.1093/cercor/bhq145

Kim, K., Rosenthal, M. Z., Gwaltney, M., Jarrold, W., Hatt, N., McIntyre, N., Swain, L., Solomon, M., & Mundy, P. (2015). A Virtual Joy-Stick Study of Emotional Responses and Social Motivation in Children with

Autism Spectrum Disorder. *Journal of Autism and Developmental Disorders*, *45*(12), 3891–3899. https://doi.org/10.1007/s10803-014-2036-7

Kirchner, J. C., Hatri, A., Heekeren, H. R., & Dziobek, I. (2011). Autistic Symptomatology, Face Processing Abilities, and Eye Fixation Patterns. *Journal of Autism and Developmental Disorders*, *41*(2), 158–167. https://doi.org/10.1007/s10803-010-1032-9

Kliemann, D., Dziobek, I., Hatri, A., Steimke, R., & Heekeren, H. R. (2010). Atypical reflexive gaze patterns on emotional faces in autism spectrum disorders. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *30*(37), 12281–12287. https://doi.org/10.1523/JNEUROSCI.0688-10.2010

Knapen, T., de Gee, J. W., Brascamp, J., Nuiten, S., Hoppenbrouwers, S., & Theeuwes, J. (2016). Cognitive and Ocular Factors Jointly Determine Pupil Responses under Equiluminance. *PLOS ONE*, *11*(5), e0155574. https://doi.org/10.1371/journal.pone.0155574

Knutson, B., Adams, C. M., Fong, G. W., & Hommer, D. (2001). Anticipation of Increasing Monetary Reward Selectively Recruits Nucleus Accumbens. *The Journal of Neuroscience*, *21*(16), RC159. https://doi.org/10.1523/JNEUROSCI.21-16-j0002.2001

Knutson, B., Taylor, J., Kaufman, M., Peterson, R., & Glover, G. (2005). Distributed Neural Representation of Expected Value. *Journal of Neuroscience*, *25*(19), 4806–4812. https://doi.org/10.1523/JNEUROSCI.0642-05.2005

Knutson, B., Westdorp, A., Kaiser, E., & Hommer, D. (2000). FMRI Visualization of Brain Activity during a Monetary Incentive Delay Task. *NeuroImage*, *12*(1), 20–27. https://doi.org/10.1006/NIMG.2000.0593

Koelewijn, T., Zekveld, A. A., Lunner, T., & Kramer, S. E. (2018). The effect of reward on listening effort as reflected by the pupil dilation response. *Hearing Research*, *367*, 106–112. https://doi.org/10.1016/J.HEARES.2018.07.011

Kohls, G., Antezana, L., Mosner, M. G., Schultz, R. T., & Yerys, B. E. (2018). Altered reward system reactivity for personalized circumscribed

interests in autism. *Molecular Autism*, *9*(1). https://doi.org/10.1186/s13229-018-0195-7

Kohls, G., Chevallier, C., Troiani, V., & Schultz, R. T. (2012). Social "wanting" dysfunction in autism: Neurobiological underpinnings and treatment implications. *Journal of Neurodevelopmental Disorders*, *4*(10). https://doi.org/10.1186/1866-1955-4-10

Kohls, G., Peltzer, J., Herpertz-Dahlmann, B., & Konrad, K. (2009). Differential effects of social and non-social reward on response inhibition in children and adolescents. *Developmental Science*, *12*(4), 614–625. https://doi.org/10.1111/j.1467-7687.2009.00816.x

Kohls, G., Peltzer, J., Schulte-Rüther, M., Kamp-Becker, I., Remschmidt, H., Herpertz-Dahlmann, B., & Konrad, K. (2011). Atypical brain responses to reward cues in autism as revealed by event-related potentials. *Journal of Autism and Developmental Disorders*, *41*(11), 1523–2533. https://doi.org/10.1007/s10803-011-1177-1

Kohls, G., Schulte-Rüther, M., Nehrkorn, B., Müller, K., Fink, G. R., Kamp-Becker, I., Herpertz-Dahlmann, B., Schultz, R. T., & Konrad, K. (2013). Reward system dysfunction in autism spectrum disorders. *Social Cognitive and Affective Neuroscience*, *8*, 565–572. https://doi.org/10.1093/scan/nss033

Kohls, G., Thönessen, H., Bartley, G. K., Grossheinrich, N., Fink, G. R., Herpertz-Dahlmann, B., & Konrad, K. (2014). Differentiating neural reward responsiveness in autism versus ADHD. *Developmental Cognitive Neuroscience*, *10*, 104–116. https://doi.org/10.1016/j.dcn.2014.08.003

Kohls, G., Yerys, B., & Schultz, R. T. (2014). Striatal development in autism: Repetitive behaviors and the reward circuitry. *Biological Psychiatry*, *76*(5), 358–359. https://doi.org/10.1016/j.biopsych.2014.07.010

Krach, S., Paulus, F. M., Bodden, M., & Kircher, Ti. (2010). The rewarding nature of social interactions. *Frontiers in Behavioral Neuroscience*, *4*, 22. https://doi.org/10.3389/fnbeh.2010.00022

Kret, M. E., & Sjak-Shie, E. E. (2018). Preprocessing pupil size data: Guidelines and code. *Behavior Research Methods*, *51*(3), 1336–1342. https://doi.org/10.3758/s13428-018-1075-y

Kujawa, A., Arfer, K. B., Klein, D. N., & Proudfit, G. H. (2014). Electrocortical reactivity to social feedback in youth: A pilot study of the Island Getaway task. *Developmental Cognitive Neuroscience*, *10*, 140–147. https://doi.org/10.1016/j.dcn.2014.08.008

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software*, *82*(13), R package version 2.0-6. https://doi.org/10.18637/jss.v082.i13

LaBar, K. S., Crupain, M. J., Voyvodic, J. T., & McCarthy, G. (2003). Dynamic perception of facial affect and identity in the human brain. *Cerebral Cortex (New York, N.Y.: 1991)*, *13*(10), 1023–1033. https://doi.org/10.1093/cercor/13.10.1023

Lai, M.-C., Kassee, C., Besney, R., Bonato, S., Hull, L., Mandy, W., Szatmari, P., & Ameis, S. H. (2019). Prevalence of co-occurring mental health diagnoses in the autism population: A systematic review and meta-analysis. *The Lancet. Psychiatry*, *6*(10), 819–829. https://doi.org/10.1016/S2215-0366(19)30289-5

Lakens, D., McLatchie, N., Isager, P. M., Scheel, A. M., & Dienes, Z. (2020). Improving Inferences About Null Effects With Bayes Factors and Equivalence Tests. *The Journals of Gerontology. Series B, Psychological Sciences and Social Sciences*, *75*(1), 45–57. https://doi.org/10.1093/geronb/gby065

Lakens, D., Scheel, A. M., & Isager, P. M. (2018). Equivalence Testing for Psychological Research: A Tutorial. *Advances in Methods and Practices in Psychological Sciences*, *1*(2), 259–269. https://doi.org/10.1177/2515245918770963

Lander, K., & Metcalfe, S. (2007). The influence of positive and negative facial expressions on face familiarity. *Memory*, *15*(1), 63–69. https://doi.org/10.1080/09658210601108732

Larson, M. J., South, M., Krauskopf, E., Clawson, A., & Crowley, M. J. (2011). Feedback and reward processing in high-functioning autism. *Psychiatry Research*, *187*(1–2), 198–203. https://doi.org/10.1016/j.psychres.2010.11.006

Leary, M. R., & Allen, A. B. (2011). Belonging motivation: Establishing, maintaining, and repairing relational value. In D. Dunning (Ed.), *Social motivation* (pp. 37–55). Psychology Press.

Lee, W. (2016). Insular Cortex Activity as the Neural Base of Intrinsic Motivation. In *Recent Developments in Neuroscience Research on Human Motivation* (Vol. 19, pp. 127–148). Emerald Group Publishing Limited. https://doi.org/10.1108/S0749-742320160000019016

Lehner, R., Balsters, J. H., Herger, A., Hare, T. A., & Wenderoth, N. (2017). Monetary, Food, and Social Rewards Induce Similar Pavlovian-to-Instrumental Transfer Effects. *Frontiers in Behavioral Neuroscience*, *10*, 247. https://doi.org/10.3389/fnbeh.2016.00247

Leiner, D. J. (2019). *SoSci Survey (Version 3.1.06)*. SoSci Survey.

Lerner, M. D., & Mikami, A. Y. (2012). A Preliminary Randomized Controlled Trial of Two Social Skills Interventions for Youth With High-Functioning Autism Spectrum Disorders. *Focus on Autism and Other Developmental Disabilities*, *27*(3), 147–157. https://doi.org/10.1177/1088357612450613

Leroy, A., Amad, A., D'Hondt, F., Pins, D., Jaafari, N., Thomas, P., & Jardri, R. (2020). Reward anticipation in schizophrenia: A coordinate-based meta-analysis. *Schizophrenia Research*, *218*, 2–6. https://doi.org/10.1016/j.schres.2019.12.041

Levy, D. J., & Glimcher, P. W. (2011). Comparing Apples and Oranges: Using Reward-Specific and Reward-General Subjective Value Representation in the Brain. *Journal of Neuroscience*, *31*(41), 14693–14707. https://doi.org/10.1523/JNEUROSCI.2218-11.2011

Liccione, D., Moruzzi, S., Rossi, F., Manganaro, A., Porta, M., Nugrahaningsih, N., Caserio, V., & Allegri, N. (2014). Familiarity is not notoriety:

Phenomenological accounts of face recognition. *Frontiers in Human Neuroscience*, *8*, 672. https://doi.org/10.3389/fnhum.2014.00672

Liebal, K., Colombi, C., Rogers, S. J., Warneken, F., & Tomasello, M. (2008). Helping and Cooperation in Children with Autism. *Journal of Autism and Developmental Disorders*, *38*(2), 224–238. https://doi.org/10.1007/s10803-007-0381-5

Liebowitz, M. R. (1987). Social Phobia. *Modern Problems of Pharmapsychiatry*, *22*, 141–173.

Liebowitz, M. R., Gorman, J. M., Fyer, A. J., & Klein, D. F. (1985). Social Phobia: Review of a Neglected Anxiety Disorder. *Archives of General Psychiatry*, *42*(7), 729–736. https://doi.org/10.1001/archpsyc.1985.01790300097013

Lin, A., Adolphs, R., & Rangel, A. (2012). Social and monetary reward learning engage overlapping neural substrates. *Social Cognitive and Affective Neuroscience*, *7*(3), 274–281. https://doi.org/10.1093/scan/nsr006

Lin, A., Rangel, A., & Adolphs, R. (2012). Impaired Learning of Social Compared to Monetary Rewards in Autism. *Frontiers in Neuroscience*, *6*, 143. https://doi.org/10.3389/fnins.2012.00143

Linnet, J. (2014). Neurobiological underpinnings of reward anticipation and outcome evaluation in gambling disorder. *Frontiers in Behavioral Neuroscience*, *8*, 100. https://doi.org/10.3389/fnbeh.2014.00100

Liu, X., Hairston, J., Schrier, M., & Fan, J. (2011). Common and distinct networks underlying reward valence and processing stages: A meta-analysis of functional neuroimaging studies. *Neurosci Biobehav Rev*, *35*(5), 1219–1236. https://doi.org/10.1016/j.neubiorev.2010.12.012

Liu, Y., Rodenkirch, C., Moskowitz, N., Schriver, B., & Wang, Q. (2017). Dynamic Lateralization of Pupil Dilation Evoked by Locus Coeruleus Activation Results from Sympathetic, Not Parasympathetic, Contributions. *Cell Reports*, *20*(13). https://doi.org/10.1016/j.celrep.2017.08.094

Lord, C., Risi, S., Lambrecht, L., Cook, E. H., Leventhal, B. L., DiLavore, P. C., Pickles, A., & Rutter, M. (2000). The Autism Diagnostic Observation Schedule—Generic: A Standard Measure of Social and

Communication Deficits Associated with the Spectrum of Autism. *Journal of Autism and Developmental Disorders*, *30*(3), 205–223. https://doi.org/10.1023/A:1005592401947

Lord, C., Rutter, M., & Le Couteur, A. (1994). Autism Diagnostic Interview-Revised: A revised version of a diagnostic interview for caregivers of individuals with possible pervasive developmental disorders. *Journal of Autism and Developmental Disorders*, *24*(5), 659–685. https://doi.org/10.1007/BF02172145

Lüdecke, D. (2020). SjPlot: SjPlot—Data visualization for statistics in social science. *R Package Version 2.8.4*.

Lundström, S., Chang, Z., Råstam, M., Gillberg, C., Larsson, H., Anckarsäter, H., & Lichtenstein, P. (2012). Autism Spectrum Disorders and Autistic-like Traits: Similar Etiology in the Extreme End and the Normal Variation. *Archives of General Psychiatry*, *69*(1), 46–52. https://doi.org/10.1001/archgenpsychiatry.2011.144

Masi, A., DeMayo, M. M., Glozier, N., & Guastella, A. J. (2017). An Overview of Autism Spectrum Disorder, Heterogeneity and Treatment Options. *Neuroscience Bulletin*, *33*(2), 183–193. https://doi.org/10.1007/s12264-017-0100-y

Mathôt, S. (2018). Pupillometry: Psychology, Physiology, and Function. *Journal of Cognition*, *1*(1), 16. https://doi.org/10.5334/joc.18

Matyjek, M., Bayer, M., & Dziobek, I. (2020). Autistic Traits Affect Reward Anticipation but not Reception. *Scientific Reports*, *10*(1), 8396. https://doi.org/10.1038/s41598-020-65345-x

Matyjek, M., Bayer, M., & Dziobek, I. (2021). Pupillary Responses to Faces Are Modulated by Familiarity and Rewarding Context. *Brain Sciences*, *11*(6), 794. https://doi.org/10.3390/brainsci11060794

Matyjek, M., Kroczek, B., & Senderecka, M. (2021). Socially induced negative affective knowledge modulates early face perception but not gaze cueing of attention. *Psychophysiology*, *58*(9), e13876. https://doi.org/10.1111/psyp.13876

Matyjek, M., Meliss, S., Dziobek, I., & Murayama, K. (2020). A Multidimensional View on Social and Non-Social Rewards. *Frontiers in Psychiatry*, *11*, 818. https://doi.org/10.3389/fpsyt.2020.00818

Mazzone, L., Ruta, L., & Reale, L. (2012). Psychiatric comorbidities in asperger syndrome and high functioning autism: Diagnostic challenges. *Annals of General Psychiatry*, *11*(1), 16. https://doi.org/10.1186/1744-859X-11-16

McPartland, J. C., Crowley, M. J., Perszyk, D. R., Mukerji, C. E., Naples, A. J., Wu, J., & Mayes, L. C. (2012). Preserved reward outcome processing in ASD as revealed by event-related potentials. *Journal of Neurodevelopmental Disorders*, *4*(1), 1–9. https://doi.org/10.1186/1866-1955-4-16

Mitchell, M. R., Berridge, K. C., & Mahler, S. V. (2018). Endocannabinoid-Enhanced "Liking" in Nucleus Accumbens Shell Hedonic Hotspot Requires Endogenous Opioid Signals. *Cannabis and Cannabinoid Research*, *3*(1), 166–170. https://doi.org/10.1089/can.2018.0021

Moser, J. S., Huppert, J. D., Duval, E., & Simons, R. F. (2008). Face processing biases in social anxiety: An electrophysiological study. *Biological Psychology*, *78*(1), 93–103. https://doi.org/10.1016/j.biopsycho.2008.01.005

Munafò, M. R., Nosek, B. A., M Bishop, D. V., Button, K. S., Chambers, C. D., Percie du Sert, N., Simonsohn, U., Wagenmakers, E.-J., Ware, J. J., & A Ioannidis, J. P. (2017). A manifesto for reproducible science. *Nature Human Behaviour*, *1*(1), 1–9. https://doi.org/10.1038/s41562-016-0021

Mundy, P., & Neal, A. R. (2000). Neural plasticity, joint attention, and a transactional social-orienting model of autism. In *International Review of Research in Mental Retardation* (Vol. 23, pp. 139–168). Academic Press. https://doi.org/10.1016/S0074-7750(00)80009-9

Murayama, K. (2019). Neuroscientific and Psychological Approaches to Incentives: Commonality and Multifaceted Views. In K. Renninger & S. Hidi (Eds.), *The Cambridge Handbook of Motivation and Learning* (pp. 141–162). University Press.

Murdoch, J. D., & State, M. W. (2013). Recent developments in the genetics of autism spectrum disorders. *Current Opinion in Genetics & Development*, *23*(3), 310–315. https://doi.org/10.1016/j.gde.2013.02.003

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*(2), 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

Natu, V., & O'Toole, A. J. (2011). The neural processing of familiar and unfamiliar faces: A review and synopsis. *British Journal of Psychology*, *102*(4), 726–747. https://doi.org/10.1111/j.2044-8295.2011.02053.x

Neuhaus, E., Beauchaine, T. P., & Bernier, R. (2010). Neurobiological correlates of social functioning in autism. *Clinical Psychology Review*, *30*(6), 733–748. https://doi.org/10.1016/j.cpr.2010.05.007

Neuhaus, E., Bernier, R. A., & Beauchaine, T. P. (2015). Electrodermal Response to Reward and Non-Reward Among Children With Autism. *Autism Research*, *8*(4), 357–370. https://doi.org/10.1002/aur.1451

Newschaffer, C. J., & Curran, L. K. (2003). Autism: An emerging public health problem. *Public Health Reports*, *118*(5), 393–399. https://doi.org/10.1093/phr/118.5.393

Nieuwenhuis, S., Aston-Jones, G., & Cohen, J. D. (2005). Decision Making, the P3, and the Locus Coeruleus–Norepinephrine System. *Psychological Bulletin*, *131*(4), 510–532. https://doi.org/10.1037/0033-2909.131.4.510

Nomi, J. S., & Uddin, L. Q. (2015). Face processing in autism spectrum disorders: From brain regions to brain networks. *Neuropsychologia*, *71*, 201–216. https://doi.org/10.1016/j.neuropsychologia.2015.03.029

Novak, K. D., & Foti, D. (2015). Teasing apart the anticipatory and consummatory processing of monetary incentives: An event-related potential study of reward dynamics. *Psychophysiology*, *52*, 1470–1482. https://doi.org/10.1111/psyp.12504

Nuske, H. J., Vivanti, G., & Dissanayake, C. (2013). Are emotion impairments unique to, universal, or specific in autism spectrum disorder? A

comprehensive review. *Cognition and Emotion*, *27*(6), 1042–1061. https://doi.org/10.1080/02699931.2012.762900

Nuske, H. J., Vivanti, G., & Dissanayake, C. (2014). Reactivity to fearful expressions of familiar and unfamiliar people in children with autism: An eye-tracking pupillometry study. *Journal of Neurodevelopmental Disorders*, *6*(1), 14. https://doi.org/10.1186/1866-1955-6-14

O'Doherty, J., Kringelbach, M. L., Rolls, E. T., Hornak, J., & Andrews, C. (2001). Abstract reward and punishment representations in the human orbitofrontal cortex. *Neuroscience*, *4*(1), 95–102. https://doi.org/10.1038/82959

O'Doherty, J., Rolls, E. T., Francis, S., Bowtell, R., McGlone, F., Kobal, G., Renner, B., & Ahne, G. (2000). Sensory-specific satiety-related olfactory activation of the human orbitofrontal cortex. *NeuroReport*, *11*(2), 399–403. https://doi.org/10.1097/00001756-200002070-00035

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*(1), 97–113. https://doi.org/10.1016/0028-3932(71)90067-4

Ortigue, S., Bianchi-Demicheli, F., De, A. F., Hamilton, C., & Grafton, S. T. (2007). The Neural Basis of Love as a Subliminal Prime: An Event-related Functional Magnetic Resonance Imaging Study. *Journal of Cognitive Neuroscience*, *19*(7), 1218–1230. https://doi.org/10.1162/jocn.2007.19.7.1218

Ouimet, A. J., Gawronski, B., & Dozois, D. J. A. (2009). Cognitive vulnerability to anxiety: A review and an integrative model. *Clinical Psychology Review*, *29*(6), 459–470. https://doi.org/10.1016/j.cpr.2009.05.004

Oumeziane, B. A., Schryer-Praga, J., & Foti, D. (2017). "Why don't they 'like' me more?": Comparing the time courses of social and monetary reward processing. *Neuropsychologia*, *107*, 48–59. https://doi.org/10.1016/j.neuropsychologia.2017.11.001

Panasiti, M. S., Puzzo, I., & Chakrabarti, B. (2016). Autistic Traits Moderate the Impact of Reward Learning on Social Behaviour. *Autism Research*, *9*, 471–479. https://doi.org/10.1002/aur.1523

Pankert, A., Pankert, K., Herpertz-Dahlmann, B., Konrad, K., & Kohls, G. (2014). Responsivity to familiar versus unfamiliar social reward in children with autism. *Journal of Neural Transmission*, *121*(9), 1199–1210. https://doi.org/10.1007/s00702-014-1210-6

Paul, K., Vassena, E., Severo, M. C., & Pourtois, G. (2020). Dissociable effects of reward magnitude on fronto-medial theta and FRN during performance monitoring. *Psychophysiology*, *57*(2), e13481. https://doi.org/10.1111/psyp.13481

Pek, J., & Flora, D. B. (2018). Reporting effect sizes in original psychological research: A discussion and tutorial. *Psychological Methods*, *23*(2), 208–225. https://doi.org/10.1037/met0000126

Perdikis, D., Volhard, J., Müller, V., Kaulard, K., Brick, T. R., Wallraven, C., & Lindenberger, U. (2017). Brain synchronization during perception of facial emotional expressions with natural and unnatural dynamics. *PloS One*, *12*(7), e0181225. https://doi.org/10.1371/journal.pone.0181225

Pernet, C. (2016). Null hypothesis significance testing: A short tutorial. *F1000Research*, *4*, 621. https://doi.org/10.12688/f1000research.6963.3

Peters, J., & Büchel, C. (2010). Neural representations of subjective reward value. *Behavioural Brain Research*, *213*(2), 135–141. https://doi.org/10.1016/j.bbr.2010.04.031

Pfabigan, D. M., Gittenberger, M., & Lamm, C. (2019). Social dimension and complexity differentially influence brain responses during feedback processing. *Social Neuroscience*, *14*(1), 26–40. https://doi.org/10.1080/17470919.2017.1395765

Pfabigan, D. M., & Han, S. (2019). Converging electrophysiological evidence for a processing advantage of social over nonsocial feedback. *Cognitive, Affective, & Behavioral Neuroscience*, *19*(5), 1170–1183. https://doi.org/10.3758/s13415-019-00737-9

Pierce, K., Haist, F., Sedaghat, F., & Courchesne, E. (2004). The brain response to personally familiar faces in autism: Findings of fusiform activity

and beyond. *Brain*, *127*, 2703–2716. https://doi.org/10.1093/brain/awh289

Pierce, K., & Redcay, E. (2008). Fusiform Function in Children with an Autism Spectrum Disorder Is a Matter of "Who." *Biological Psychiatry*, *64*(7), 552–560. https://doi.org/10.1016/j.biopsych.2008.05.013

Poldrack, R. A. (2006). Can cognitive processes be inferred from neuroimaging data? *Trends in Cognitive Sciences*, *10*(2), 59–63. https://doi.org/10.1016/j.tics.2005.12.004

Preston, S. D., & de Waal, F. B. M. (2002). Empathy: Its ultimate and proximate bases. *Behavioral and Brain Sciences*, *25*(1), 1–20. https://doi.org/10.1017/S0140525X02000018

Preuschoff, K., 't Hart, B. M., & Einhauser, W. (2011). Pupil dilation signals surprise: Evidence for noradrenaline's role in decision making. *Frontiers in Neuroscience*, *5*, 115. https://doi.org/10.3389/fnins.2011.00115

Puzzo, I., Cooper, N. R., Vetter, P., & Russo, R. (2010). EEG activation differences in the pre-motor cortex and supplementary motor area between normal individuals with high and low traits of autism. *Brain Research*, *1342*, 104–110. https://doi.org/10.1016/j.brainres.2010.04.060

R Core Team. (2017). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. http://www.r-project.org

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. http://www.r-project.org/

Rademacher, L., Krach, S., Kohls, G., Irmak, A., Gründer, G., & Spreckelmeyer, K. N. (2010). Dissociation of neural networks for anticipation and consumption of monetary and social rewards. *NeuroImage*, *49*(4), 3276–3285. https://doi.org/10.1016/J.NEUROIMAGE.2009.10.089

Ramon, M., & Gobbini, M. I. (2018). Familiarity matters: A review on prioritized processing of personally familiar faces. *Visual Cognition*, *26*(3), 179–195. https://doi.org/10.1080/13506285.2017.1405134

Redcay, E., Rice, K., & Saxe, R. (2013). Interaction versus observation: A finer look at this distinction and its importance to autism. *Behavioral and*

Brain Sciences, *36*(4), 435–435. https://doi.org/10.1017/S0140525X12002026

Richard, F. D., Bond, C. F., & Stokes-Zoota, J. J. (2003). One Hundred Years of Social Psychology Quantitatively Described. *Review of General Psychology*, *7*(4), 331–363. https://doi.org/10.1037/1089-2680.7.4.331

Richey, J. A., Rittenberg, A., Hughes, L., Damiano, C. R., Sabatino, A., Miller, S., Hanna, E., Bodfish, J. W., & Dichter, G. S. (2014). Common and distinct neural features of social and non-social reward processing in autism and social anxiety disorder. *Social Cognitive and Affective Neuroscience*, *9*(3), 367–377. https://doi.org/10.1093/scan/nss146

Rights, J. D., & Sterba, S. K. (2018). Quantifying Explained Variance in Multilevel Models: An Integrative Framework for Defining R-Squared Measures. *Psychological Methods*, *24*(3), 309. https://doi.org/10.1037/met0000184

Rilling, J. K., Gutman, D. A., Zeh, T. R., Pagnoni, G., Berns, G. S., & Kilts, C. D. (2002). A Neural Basis for Social Cooperation. *Neuron*, *35*(2), 395–405. https://doi.org/10.1016/S0896-6273(02)00755-9

Risko, E. F., Laidlaw, K. E., Freeth, M., Foulsham, T., & Kingstone, A. (2012). Social attention with real versus reel stimuli: Toward an empirical approach to concerns about ecological validity. *Frontiers in Human Neuroscience*, *6*, 143. https://doi.org/10.3389/fnhum.2012.00143

Robinson, T. E., & Berridge, K. C. (1993). The neural basis of drug craving: An incentive-sensitization theory of addiction. *Brain Research Reviews*, *18*(3), 247–291. https://doi.org/10.1016/0165-0173(93)90013-P

Rolison, M. J., Naples, A. J., Rutherford, H. J. V., & McPartland, J. C. (2017). Modulation of reward in a live social context as revealed through interactive social neuroscience. *Social Neuroscience*, *13*(4), 1–13. https://doi.org/10.1080/17470919.2017.1339635

Rosell-Negre, P., Bustamante, J. C., Fuentes-Claramonte, P., Costumero, V., Benabarre, S., & Barrós-Loscertales, A. (2017). Monetary reward magnitude effects on behavior and brain function during goal-directed

behavior. *Brain Imaging and Behavior*, *11*(4), 1037–1049. https://doi.org/10.1007/s11682-016-9577-7

Ruff, C. C., & Fehr, E. (2014). The neurobiology of rewards and values in social decision making. *Nature Reviews Neuroscience*, *15*(8), 549–562. https://doi.org/10.1038/nrn3776

Ruta, L., Famà, F. I., Bernava, G. M., Leonardi, E., Tartarisco, G., Falzone, A., Pioggia, G., & Chakrabarti, B. (2017). Reduced preference for social rewards in a novel tablet based task in young children with Autism Spectrum Disorders. *Scientific Reports*, *7*, 3329. https://doi.org/10.1038/s41598-017-03615-x

Ruzich, E., Allison, C., Smith, P., Watson, P., Auyeung, B., Ring, H., & Baron-Cohen, S. (2015). Measuring autistic traits in the general population: A systematic review of the Autism-Spectrum Quotient (AQ) in a non-clinical population sample of 6,900 typical adult males and females. *Molecular Autism*, *6*(1), 1–12. https://doi.org/10.1186/2040-2392-6-2

Sasson, N. J., Dichter, G. S., & Bodfish, J. W. (2012). Affective Responses by Adults with Autism Are Reduced to Social Images but Elevated to Images Related to Circumscribed Interests. *PLOS ONE*, *7*(8), e42457. https://doi.org/10.1371/journal.pone.0042457

Saxe, R., & Haushofer, J. (2008). For Love or Money: A Common Neural Currency for Social and Monetary Reward. *Neuron*, *58*(2), 164–165. https://doi.org/10.1016/j.neuron.2008.04.005

Schilbach, L., Timmermans, B., Reddy, V., Costall, A., Bente, G., Schlicht, T., & Vogeley, K. (2013). Toward a second-person neuroscience. *Behavioral and Brain Sciences*, *36*(4), 393–414. https://doi.org/10.1017/S0140525X12000660

Schmitz, N., Rubia, K., Van Amelsvoort, T., Daly, E., Smith, A., & Murphy, D. G. M. (2008). Neural correlates of reward in autism. *The British Journal of Psychiatry*, *192*, 19–24. https://doi.org/10.1192/bjp.bp.107.036921

Schneider, M., Leuchs, L., Czisch, M., Sämann, P. G., & Spoormaker, V. I. (2018). Disentangling reward anticipation with simultaneous

pupillometry / fMRI. *NeuroImage*, *178*, 11–22. https://doi.org/10.1016/j.neuroimage.2018.04.078

Schultz, R. T. (2005). Developmental deficits in social perception in autism: The role of the amygdala and fusiform face area. *International Journal of Developmental Neuroscience*, *23*(2–3), 125–141. https://doi.org/10.1016/j.ijdevneu.2004.12.012

Schultz, W. (2015). Neuronal Reward and Decision Signals: From Theories to Data. *Physiological Reviews*, *95*(3), 853–951. https://doi.org/10.1152/physrev.00023.2014

Schwarz, K., Moessnang, C., Schweiger, J. I., Baumeister, S., Plichta, M. M., Brandeis, D., Banaschewski, T., Wackerhagen, C., Erk, S., Walter, H., Tost, H., & Meyer-Lindenberg, A. (2020). Transdiagnostic Prediction of Affective, Cognitive, and Social Function Through Brain Reward Anticipation in Schizophrenia, Bipolar Disorder, Major Depression, and Autism Spectrum Diagnoses. *Schizophrenia Bulletin*, *46*(3), 592–602. https://doi.org/10.1093/schbul/sbz075

Scott-Van Zeeland, A. A., Dapretto, M., Ghahremani, D. G., Poldrack, R. A., & Bookheimer, S. Y. (2010). Reward processing in autism. *Autism Research*, *3*(2), 53–67. https://doi.org/10.1002/aur.122

Seeley, W. W., Menon, V., Schatzberg, A. F., Keller, J., Glover, G. H., Kenna, H., Reiss, A. L., & Greicius, M. D. (2007). Dissociable Intrinsic Connectivity Networks for Salience Processing and Executive Control. *Journal of Neuroscience*, *27*(9), 2349–2356. https://doi.org/10.1523/JNEUROSCI.5587-06.2007

Senderecka, M., Matyjek, M., Kroczek, B., & Ociepka, M. (2021). Socially induced negative emotions elicit neural activity in the mentalizing network in a subsequent inhibitory task. *Neuroscience*, *470*, 1–15. https://doi.org/10.1016/j.neuroscience.2021.06.032

Sepeta, L., Tsuchiya, N., Davies, M. S., Sigman, M., Bookheimer, S. Y., & Dapretto, M. (2012). Abnormal social reward processing in autism as indexed by pupillary responses to happy faces. *Journal of Neurodevelopmental Disorders*, *4*(1), 1–9. https://doi.org/10.1186/1866-1955-4-17

Sescousse, G., Redouté, J., & Dreher, J.-C. (2010). The Architecture of Reward Value Coding in the Human Orbitofrontal Cortex. *Journal of Neuroscience*, *30*(39), 13095–13104. https://doi.org/10.1523/JNEUROSCI.3501-10.2010

Shafritz, K. M., Bregman, J. D., Ikuta, T., & Szeszko, P. R. (2015). Neural systems mediating decision-making and response inhibition for social and nonsocial stimuli in autism. *Progress in Neuro-Psychopharmacology and Biological Psychiatry*, *60*, 112–120. https://doi.org/10.1016/j.pnpbp.2015.03.001

Silva, C., Da Fonseca, D., Esteves, F., & Deruelle, C. (2015). Motivational approach and avoidance in autism spectrum disorder: A comparison between real photographs and cartoons. *Research in Autism Spectrum Disorders*, *17*, 13–24. https://doi.org/10.1016/j.rasd.2015.05.004

Simonoff, E., & Chandler, S. (2008). Psychiatric Disorders in Children With Autism Spectrum Disorders: Prevalence, Comorbidity, and Associated Factors in a Population-Derived Sample. *Journal of the American Academy of Child & Adolescent Psychiatry*, *47*(8), 921–929. https://doi.org/10.1097/CHI.0b013e318179964f

Sims, T. B., Neufeld, J., Johnstone, T., & Chakrabarti, B. (2013). Autistic traits modulate frontostriatal connectivity during processing of rewarding faces. *Social Cognitive and Affective Neuroscience*, *9*(12), 2010–2016. https://doi.org/10.1093/scan/nsu010

Sims, T. B., Van Reekum, C. M., Johnstone, T., & Chakrabarti, B. (2012). How reward modulates mimicry: EMG evidence of greater facial mimicry of more rewarding happy faces. *Psychophysiology*, *49*(7), 998–1004. https://doi.org/10.1111/j.1469-8986.2012.01377.x

Skinner, B. F. (1938). *The Behavior of Organisms: An Experimental Analysis*. D. Appleton-Century Company.

Smith, B. W., Mitchell, D. G. V., Hardin, M. G., Jazbec, S., Fridberg, D., Blair, R. J. R., & Ernst, M. (2009). Neural substrates of reward magnitude, probability, and risk during a wheel of fortune decision-making task. *NeuroImage*, *44*(2), 600–609. https://doi.org/10.1016/j.neuroimage.2008.08.016

Smith, D. V., Hayden, B. Y., Truong, T.-K., Song, A. W., Platt, M. L., & Huettel, S. A. (2010). Distinct Value Signals in Anterior and Posterior Ventromedial Prefrontal Cortex. *The Journal of Neuroscience*, *30*(7), 2490–2495. https://doi.org/10.1523/JNEUROSCI.3319-09.2010

South, M., Dana, J., White, S. E., & Crowley, M. J. (2011). Failure is not an option: Risk-taking is moderated by anxiety and also by cognitive ability in children and adolescents diagnosed with an autism spectrum disorder. *Journal of Autism and Developmental Disorders*, *41*(1), 55–65. https://doi.org/10.1007/s10803-010-1021-z

South, M., Larson, M. J., Krauskopf, E., & Clawson, A. (2010). Error processing in high-functioning Autism Spectrum Disorders. *Biological Psychology*, *85*(2), 242–251. https://doi.org/10.1016/j.biopsycho.2010.07.009

Spain, D., Sin, J., Linder, K. B., McMahon, J., & Happé, F. (2018). Social anxiety in autism spectrum disorder: A systematic review. *Research in Autism Spectrum Disorders*, *52*, 51–68. https://doi.org/10.1016/J.RASD.2018.04.007

Speelman, C., Smithson, M., Campitelli, G., Lo, S., & Andrews, S. (2015). To transform or not to transform: Using generalized linear mixed models to analyse reaction time data. *Frontiers in Psychology*, *6*, 1171. https://doi.org/10.3389/fpsyg.2015.01171

Spreckelmeyer, K. N., Krach, S., Kohls, G., Rademacher, L., Irmak, A., Konrad, K., Kircher, T., & Gründer, G. (2009). Anticipation of monetary and social reward differently activates mesolimbic brain structures in men and women. *Social Cognitive and Affective Neuroscience*, *4*(2), 158–165. https://doi.org/10.1093/scan/nsn051

Spreckelmeyer, K. N., Rademacher, L., Paulus, F. M., & Gründer, G. (2013). Neural activation during anticipation of opposite-sex and same-sex faces in heterosexual men and women. *NeuroImage*, *66*, 223–231. https://doi.org/10.1016/j.neuroimage.2012.10.068

Stavropoulos, K. K. M., & Carver, L. J. (2014a). Effect of Familiarity on Reward Anticipation in Children with and without Autism Spectrum

Disorders. *PLoS ONE*, *9*(9), e106667. https://doi.org/10.1371/journal.pone.0106667

Stavropoulos, K. K. M., & Carver, L. J. (2014b). Reward anticipation and processing of social versus nonsocial stimuli in children with and without autism spectrum disorders. *Journal of Child Psychology and Psychiatry*, *55*(12), 1398–1408. https://doi.org/10.1111/jcpp.12270

Stavropoulos, K. K. M., Viktorinova, M., Naples, A., Foss-Feig, J., & Mcpartland, J. C. (2018). Autistic traits modulate conscious and nonconscious face perception. *Social Neuroscience*, *13*(1), 40–51. https://doi.org/10.1080/17470919.2016.1248788

Sugiura, M. (2014). Neuroimaging studies on recognition of personally familiar people. *Frontiers in Bioscience*, *19*, 672–686. https://doi.org/10.2741/4235

Takarada, Y., & Nozaki, D. (2017). Pupil dilations induced by barely conscious reward goal-priming. *Neuropsychologia*, *103*, 69–76. https://doi.org/10.1016/J.NEUROPSYCHOLOGIA.2017.07.020

Taylor, S. C., Steeman, S., Gehringer, B. N., Dow, H. C., Langer, A., Rawot, E., Perez, L., Goodman, M., Smernoff, Z., Grewal, M., Eshraghi, O., Pallathra, A. A., Oksas, C., Mendez, M., Gur, R. C., Rader, D. J., Bucan, M., Almasy, L., & Brodkin, E. S. (2021). Heritability of quantitative autism spectrum traits in adults: A family-based study. *Autism Research*, *14*(8), 1543–1553. https://doi.org/10.1002/aur.2571

Thibaut, J. W., & Kelley, H. H. (1959). *The Social Psychology of Groups*. Routledge. https://doi.org/10.4324/9781315135007

Thompson, E. (2010). *Mind in Life: Biology, Phenomenology, and the Sciences of Mind*. Harvard University Press.

Tobler, P. N., & Kobayashi, S. (2009). Electrophysiological correlates of reward processing in dopamine neurons. In J.-C. Dreher & L. Tremblay (Eds.), *Handbook of Reward and Decision Making* (pp. 29–50). Academic Press. https://doi.org/10.1016/B978-0-12-374620-7.00002-9

Todorov, A. (2012). The role of the amygdala in face perception and evaluation. *Motivation and Emotion*, *36*(1), 16–26. https://doi.org/10.1007/s11031-011-9238-5

van den Buuse, M. (1998). Role of the mesolimbic dopamine system in cardiovascular homeostasis. Stimulation of the ventral tegmental area modulates the effect of vasopressin on blood pressure in conscious rats. *Clinical and Experimental Pharmacology & Physiology*, *25*(9), 661–668. https://doi.org/10.1111/j.1440-1681.1998.tb02273.x

van Dongen, E. V., von Rhein, D., O'Dwyer, L., Franke, B., Hartman, C. A., Heslenfeld, D. J., Hoekstra, P. J., Oosterlaan, J., Rommelse, N., & Buitelaar, J. (2015). Distinct effects of ASD and ADHD symptoms on reward anticipation in participants with ADHD, their unaffected siblings and healthy controls: A cross-sectional study. *Molecular Autism*, *6*(1), 48. https://doi.org/10.1186/s13229-015-0043-y

van Ravenzwaaij, D., Monden, R., Tendeiro, J. N., & Ioannidis, J. P. A. (2019). Bayes factors for superiority, non-inferiority, and equivalence designs. *BMC Medical Research Methodology*, *19*(1), 71. https://doi.org/10.1186/s12874-019-0699-7

Vandierendonck, A. (2018). Further Tests of the Utility of Integrated Speed-Accuracy Measures in Task Switching. *Journal of Cognition*, *1(1)*(8), 1–16. https://doi.org/10.5334/joc.6

Verschuur, R., Didden, R., Lang, R., Sigafoos, J., & Huskens, B. (2014). Pivotal Response Treatment for Children with Autism Spectrum Disorders: A Systematic Review. *Review Journal of Autism and Developmental Disorders*, *1*(1), 34–61. https://doi.org/10.1007/s40489-013-0008-z

Visconti di Oleggio Castello, M., Guntupalli, J. S., Yang, H., & Gobbini, M. I. (2014). Facilitated detection of social cues conveyed by familiar faces. *Frontiers in Human Neuroscience*, *8*, 678. https://doi.org/10.3389/fnhum.2014.00678

Volkow, N. D., Michaelides, M., & Baler, R. (2019). The Neuroscience of Drug Reward and Addiction. *Physiological Reviews*, *99*(4), 2115–2140. https://doi.org/10.1152/physrev.00014.2018

Von Neumann, J., & Morgenstern, O. (1947). *Theory of games and economic behavior*. Princeton University Press.

Wake, S. J., & Izuma, K. (2017). A common neural code for social and monetary rewards in the human striatum. *Social Cognitive and Affective Neuroscience*, *12*(10), 1558–1564. https://doi.org/10.1093/scan/nsx092

Warneken, F., & Tomasello, M. (2008). Extrinsic Rewards Undermine Altruistic Tendencies in 20-Month-Olds. *Developmental Psychology*, *44*, 1785–1788. https://doi.org/10.1037/a0013860

Watanabe, N., Bhanji, J. P., Ohira, H., & Delgado, M. R. (2019). Reward-Driven Arousal Impacts Preparation to Perform a Task via Amygdala-Caudate Mechanisms. *Cerebral Cortex*, *29*(7), 3010–3022. https://doi.org/10.1093/cercor/bhy166

Watson, K. K., Miller, S., Hannah, E., Kovac, M., Damiano, C. R., Sabatino-DiCrisco, A., Turner-Brown, L., Sasson, N. J., Platt, M. L., & Dichter, G. S. (2015). Increased reward value of non-social stimuli in children and adolescents with autism. *Frontiers in Psychology*, *6*, 1026. https://doi.org/10.3389/fpsyg.2015.01026

White, S. W., Oswald, D., Ollendick, T., & Scahill, L. (2009). Anxiety in children and adolescents with autism spectrum disorders. *Clinical Psychology Review*, *29*(3), 216–229. https://doi.org/10.1016/j.cpr.2009.01.003

Winston, J. S., O'Doherty, J., Kilner, J. M., Perrett, D. I., & Dolan, R. J. (2007). Brain systems for assessing facial attractiveness. *Neuropsychologia*, *45*, 195–206. https://doi.org/10.1016/j.neuropsychologia.2006.05.009

Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, *73*(1), 3–36. https://doi.org/10.1111/j.1467-9868.2010.00749.x

Woodbury-Smith, M. R., Robinson, J., Wheelwright, S., & Baron-Cohen, S. (2005). Screening Adults for Asperger Syndrome Using the AQ: A Preliminary Study of its Diagnostic Validity in Clinical Practice. *Journal of*

Autism and Developmental Disorders, *35*(3), 331–335. https://doi.org/10.1007/s10803-005-3300-7

Wu, Y., & Zhou, X. (2009). The P300 and reward valence, magnitude, and expectancy in outcome evaluation. *Brain Research*, *1286*, 114–122. https://doi.org/10.1016/J.BRAINRES.2009.06.032

Yoon, H. J., Sung, S. Y., Choi, J. N., Lee, K., & Kim, S. (2015). Tangible and Intangible Rewards and Employee Creativity: The Mediating Role of Situational Extrinsic Motivation. *Creativity Research Journal*, *27*(4), 383–393. https://doi.org/10.1080/10400419.2015.1088283

Young, A. W., & Burton, A. M. (2018). Are We Face Experts? *Trends in Cognitive Sciences*, *22*(2), 100–110. https://doi.org/10.1016/J.TICS.2017.11.007

Zink, C. F., Pagnoni, G., Martin-Skurski, M. E., Chappelow, J. C., & Berns, G. S. (2004). Human Striatal Responses to Monetary Reward Depend on Saliency. *Neuron*, *42*(3), 509–517. https://doi.org/10.1016/S0896-6273(04)00183-7

Zink, C. F., Tong, Y., Chen, Q., Bassett, D. S., Stein, J. L., & Meyer-Lindenberg, A. (2008). Know Your Place: Neural Processing of Social Hierarchy in Humans. *Neuron*, *58*(2), 273–283. https://doi.org/10.1016/j.neuron.2008.01.025

Eidesstattliche Erklärung

Hiermit erkläre ich, die Dissertation selbstständig und nur unter Verwendung der angegebenen Hilfen und Hilfsmittel angefertigt zu haben. Ich habe mich anderwärts nicht um einen Doktorgrad beworben und besitze keinen entsprechenden Doktorgrad. Ich erkläre, dass ich die Dissertation oder Teile davon nicht bereits bei einer anderen wissenschaftlichen Einrichtung eingereicht habe und dass sie dort weder angenommen noch abgelehnt wurde. Ich erkläre die Kenntnisnahme der dem Verfahren zugrunde liegenden Promotionsordnung der Lebenswissenschaftlichen Fakultät der Humboldt-Universität zu Berlin vom 5. März 2015. Weiterhin erkläre ich, dass keine Zusammenarbeit mit gewerblichen Promotionsbearbeiterinnen/Promotionsberatern stattgefunden hat und dass die Grundsätze der Humboldt-Universität zu Berlin zur Sicherung guter wissenschaftlicher Praxis eingehalten wurden.

I hereby declare that I completed the doctoral thesis independently based on the stated resources and aids. I have not applied for a doctoral degree elsewhere and do not have a corresponding doctoral degree. I have not submitted the doctoral thesis, or parts of it, to another academic institution and the thesis has not been accepted or rejected. I declare that I have acknowledged the Doctoral Degree Regulations which underlie the procedure of the Faculty of Life Sciences of Humboldt-Universität zu Berlin, as amended on 5th March 2015. Furthermore, I declare that no collaboration with commercial doctoral degree supervisors took place, and that the principles of Humboldt-Universität zu Berlin for ensuring good academic practice were abided by.

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