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Spontaneous eye movements and trait empathy predict vicarious learning of fear

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ABSTRACT

Learning to predict dangerous outcomes is important to survival. In humans, this kind of learning is often transmitted through the observation of others' emotional responses. We analyzed eye movements during an observational/vicarious fear learning procedure, in which healthy participants ($N = 33$) watched another individual ('learning model') receiving aversive treatment (shocks) paired with a predictive conditioned stimulus (CS+), but not a control stimulus (CS−). Participants' gaze pattern towards the model differentiated as a function of whether the CS was predictive or not of a shock to the model. Consistent with our hypothesis that the face of a conspecific in distress can act as an unconditioned stimulus (US), we found that the total fixation time at a learning model's face increased when the CS+ was shown. Furthermore, we found that the total fixation time at the CS+ during learning predicted participants' conditioned responses (CRs) at a later test in the absence of the model. We also demonstrated that trait empathy was associated with stronger CRs, and that autistic traits were positively related to autonomic reactions to watching the model receiving the aversive treatment. Our results have implications for both healthy and dysfunctional socio-emotional learning.

1. Introduction

Learning to predict dangerous outcomes is important to survival. To understand the mechanisms underlying this learning, past research has focused the study on direct, Pavlovian, fear conditioning (LeDoux, 2012). In a fear conditioning procedure, a conditioned stimulus (CS+) is repeatedly paired with a naturally aversive unconditioned stimulus (US), such as an electric shock. The US elicits an unconditioned response (UR), which can take the form of behavioral avoidance or increased autonomic arousal. After repeated CS–US pairings, the CS will elicit a conditioned response (CR) similar to the UR.

In our socio-cultural environment, information about what is dangerous and should be avoided is commonly transmitted through other individuals by verbal communication and observation (Goubert et al., 2011; Olsson and Phelps, 2007; Rachman, 1977. This is often adaptive, because social or vicarious learning can be more effective and less dangerous than learning from individual trial and error (Rendell et al., 2010). Social transmission of fear can, however, also cause exaggerated and dysfunctional fear and anxiety, which is reflected by the inclusion of social transmission of fears and anxieties in the most recent Diagnostic and Statistical Manual of Mental Disorders (DSM 5; *American Psychiatric Association*, 2013). Previous research has shown that Pavlovian fear conditioning involves a network of brain regions, critically including the amygdala, which serves to enhance attentional allocation to the emotionally significant stimuli, and to shape CS–US associations and the ensuing CR (LeDoux, 2012; Phelps and LeDoux, 2005). In spite of a growing scientific interest in social or vicarious learning of fear in humans (Helsen et al., 2013; Olsson and Phelps, 2007) and non-human animals (Debiec and Sullivan, 2014; Jeon et al., 2010), the processes underlying the social transmission of fear remain largely unknown.

Recently, research has provided evidence that vicarious and Pavlovian fear learning is relying on partly overlapping biological mechanisms (Askew and Field, 2007; Olsson and Phelps, 2004, 2007). Accordingly, the observed individual's (the 'learning model's') expression of fear or distress can serve as a 'social' US affecting the learning through processing of social information in analogy to how tactile-sensory qualities of a Pavlovian US affect learning in direct fear conditioning. In support of this, a classical study by Mineka et al. (1984) showed that the UR–CR relationship in vicarious and Pavlovian fear learning is similar. This study demonstrated that the level of distress displayed by a model rhesus monkey in the presence of a snake was highly predictive of the subsequent level of learned fear as expressed by an observing monkey.

Vicarious fear learning should also be dependent on a range of social and cognitive factors, such as attention to salient cues in the environment that are informative of the occurrence and quality of the social US. In support of this, past research has shown that learning from others' emotional

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expressions of distress depends on the learner's perception of, and expectations about, the model, as well as the US. In an early study, Berger (1962) demonstrated that human participants acquired a CR by watching a confederate taking part in an alleged Pavlovian conditioning procedure. This, and another similar study (Hygge and Öhman, 1978), both demonstrated that the more salient the expression of the model, and the stronger the belief that the shocks were real, the stronger was the subsequent CR. These results are consistent with the finding that social learning of fear is also possible through verbal transmission alone, for example, when a person is explicitly told that a stimulus is predictive of an aversive outcome (Olsson and Phelps, 2004; Phelps et al., 2001).

Subsequent studies in humans and other species have pointed to a number of additional factors that may influence vicarious fear learning (Goubert et al., 2011). These include situation specific factors, such as tonic arousal level (Bandura and Rosenthal, 1966), empathic appraisal (Olsson et al., submitted for publication), perceived qualities of the model, such as perceived similarity (Golkar et al., 2015), and emotional expressiveness of (Goubert et al., 2011), as well as the fear-relevance of the CS (Askew and Field, 2007). Providing further clues about the underlying mechanisms, a fMRI study on vicarious fear learning (Olsson et al., 2007) showed activity in brain regions implicated in Pavlovian fear conditioning (i.e., the amygdala), as well as empathic processes (the anterior cingulate cortex, and anterior insula, Bernhardt and Singer, 2012). Importantly, activity in these regions during observation of the model's expressions when receiving shocks, predicted the strength of the CR as expressed at a later time in the absence of the model.

In accordance with the research reviewed here, attention to the learning model's emotional expressions, including facial and bodily movements, and their contingent occurrence with CS, should determine the efficiency of fear learning from vicarious experiences.

1.1. Eye-movements in emotional processing

A long line of research has documented that humans tend to direct a larger proportion of their fixations to socially and emotionally significant parts of naturalistic social scenes (Findlay and Gilchrist, 2003). Furthermore, eye movements during visual scene perception do not only reflect the actual content of the scene, but are also used to encode predictions about the actions of observed agents (Falck-Ytter et al., 2006). Analyses of eye movements can therefore be informative about how a visual scene is processed. The threat-relevance and emotional salience of visual stimuli is typically reflected in the pattern of eye movements. For example, humans fixate longer on fearful or angry faces than neutral (Green et al., 2003; Hunnius et al., 2011), make more and longer fixations towards emotionally laden scenes (Nummenmaa et al., 2006). Eippert et al. (2012) recently demonstrated that this finding extends to CS+ after Pavlovian fear conditioning. In line with this, we expected that fear learning would affect participants' gaze behavior.

The human face is a rich source of information about both mental states and the external world. The direction of another individual's gaze can effectively trigger shifts of attention to a new location. This indicates that humans follow the gaze of others to retrieve potentially important information from the surrounding environment. This is believed to constitute an important mechanism for social learning (Meltzoff et al., 2009; Tomasello, 2009). Eye movements are also likely to be important for successful recognition of facial emotion and facial memory (Henderson et al., 2005). Therefore, it is not surprising that fearful expressions in conspecifics have been shown to influence associative learning in both human and other primates (Blair, 2003; Meffert et al., 2014; Mineka and Cook, 1993; Olsson and Phelps, 2007). Given the importance of attention to human faces in social learning, we expected that participants' attention to the model's face would increase in the presence of a CS+ predictive of vicarious shocks, and that longer fixation time at the model's face would result in stronger learning.

1.2. Empathic processes and autistic traits

Autism spectrum disorder (ASD) is a neurodevelopmental condition characterized by impaired social interaction and understanding. Autistic traits are normally distributed in the population (Ronald and Hoekstra, 2011), and individuals with higher degrees of subclinical autistic traits may show some of the social cognitive characteristics of ASD (e.g. Dalton et al., 2007). One of the most studied social impairments in ASD is atypical attention to faces (Guillon et al., 2014). For example, adults with ASD are less likely than typically developed persons to direct their gaze towards the eyes of others in complex social scenes (Klin et al., 2002). Given the importance of attention to faces for efficient social learning, ASD or autistic traits would be expected to be linked to attenuated social learning of fear. Somewhat unexpectedly, subclinical autistic traits have recently been linked to stronger vicarious fear learning. Miu et al. (2012) compared fear learning in nonclinical groups with either high or low self-reported autistic traits using an observational fear learning paradigm adapted from Olsson et al. (2007). Interestingly, the participants with high autistic traits showed a stronger CR, which is surprising if the appraisal of the model's mental state is important for the ensuing learning, and the fact that autistic traits are associated with lower levels of trait empathy (Lawrence et al., 2004). The results by Miu et al. might, however, be explained by strong vicarious responses. In fact, there is evidence that individuals with ASD show at least as strong autonomic responses, and experience distress in response to distress in others, as long as they can form an adequate cognitive representation of the other's mental state (Bernhardt and Singer, 2012; Blair, 2008). Another, non-exclusive, explanation is that the high autistic traits group learned the CS–US contingencies at least as well as the low autistic group. Previous studies on Pavlovian fear learning in ASD patients has shown both intact (Bernier et al., 2005; South et al., 2011) and attenuated (Gaigg and Bowler, 2007) fear learning in ASD patients.

Empathy consists of a number of subprocesses, such as emotional contagion and empathic appraisals (Preston and De Waal, 2002). A recent study (Olsson et al., submitted for publication), demonstrated that an increase in empathic appraisal of the observed models' thoughts and feelings during observational fear learning increased the strength of the subsequent expression of the CR. This was especially true in participants high in trait empathy, suggesting that observational fear learning is influenced by individual differences in empathic ability.

To better understand vicarious fear learning, more knowledge is needed about the allocation of attention to social and emotional cues, as well as variability in trait-like abilities to process social cognitive and emotional information. These processes are likely to be important for vicarious fear learning. Here, we draw on standard psychophysiology and eye-tracking methods to examine the physiological and attentional bases of vicarious fear learning. In addition, based on past research on relevant individual differences in learning from others' thoughts and feelings, we examined the impact of trait empathy and autistic traits on this kind of social learning.

1.3. The present study

The primary aim of the present study was to explore the processes underlying vicarious fear learning by examining eye movements. We therefore examined whether participants' spontaneous allocation of gaze during vicarious fear learning was related to (1) autonomic "social" unconditioned responses (UR) to a learning model, who expressed distress when receiving electric shocks, and (2) learning measured as differential SCR to the conditioned stimuli (CS) during the subsequent test phase in the absence of the learning model. We were also interested in whether participants' eye movements to the model and the displayed scene would differ depending on whether the displayed CS was predictive or not predictive of a shock to the learning model We expected that participants would look differently at the scene as a function of which

CS was presented even in the absence of overt movements associated with the electric shocks to the model.

A secondary aim of the present study was to better understand the relationship between trait empathy, autistic traits and vicarious fear learning. We hypothesized that trait empathy would be positively correlated with the strength of the responses to vicarious shocks, and that trait empathy would be associated with stronger emotional learning. Finally, we hypothesized that trait empathy would also be associated with increased attention to the areas of the screen associated with stronger learning.

2. Methods

2.1. Participants

Thirty-nine participants were recruited through advertisement at the KI campus. Of these, six were excluded from analyses for the following reasons: use of medication (benzodiazepine) that may affect autonomic arousal ($n = 1$), a diagnosis of Asperger syndrome ($n = 1$), participation in previous experiments involving fear conditioning and electric shocks ($n = 2$), stating that a greater number of shocks had been delivered during CS− than during CS+ events, which indicated that these participants failed to understand a crucial aspect of the experimental manipulation ($n = 2$). Data from the remaining participants ($n = 33$; 15 females) were used in the analyses of skin conductance and trait measures.

Six participants (three males) were excluded from analyses of eye movements because of data loss (i.e. <20% valid data points from all events, see Section 2.4.1). One participant scored above the proposed cut-off for ASD (>21; Baron-Cohen et al., 2001), and was therefore excluded from analyses involving this measure.

2.2. Apparatus and materials

A video of about 4.5 minute length served as stimulus material for the observational learning procedure. The video showed a male model seated in front of a computer monitor (see Fig. 1). A shock electrode similar to the one that the participants were wearing was attached to the model's arm and clearly visible to the participant. Two geometric shapes visible to the participant and the model served as the conditioned stimuli. Each of these was presented six times in pseudorandom order. One of these geometric shapes (the CS+) was coupled with an electric shock to the models right arm during four of the six presentations. The other shape (the CS−) was presented an equal number of times, but was never coupled with an electric shock. The stimulus used as CS+ was counterbalanced across participants.

When a shock was administered to the model's wrist, his arm made a brief jerking movement, and he displayed a fleeting contraction of the muscles in the upper part of the face, including a blink (of about 500 ms duration). During the rest of the video, the model made no movements.

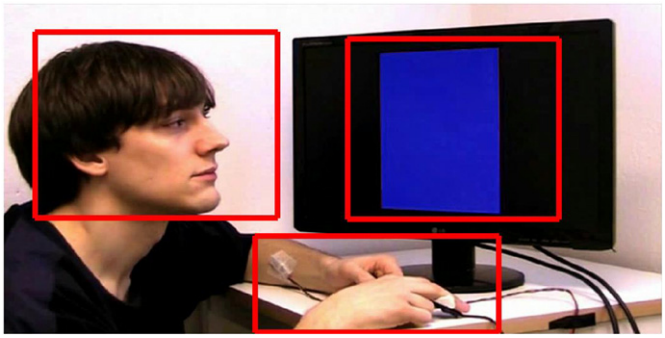

Fig. 1. Areas of interests (AOIs) used in the eye movement analyses.

The CS+ and CS− were later presented to the participant in a pseudorandom order, extending approximately 29° of the visual field in horizontal direction. Participants were seated at approximately 70 cm distance from a 24″ monitor. Eye movements were recorded with a corneal reflection eye tracker (iView X RED, Sensomotoric Systems GmbH) at a sample rate of 50 Hz. Participants were seated at approximately 70 cm distance from a 24″ monitor. All participants completed a 16 point operator-controlled calibration procedure at the beginning of the experiment. Skin conductance data were recorded at a sample rate of 250 Hz with a Biopac MP150 system at palmar sites of the participants' non-dominant hand.

2.3. Procedure

The experimental procedure was adapted from Olsson & Phelps (2004) and Olsson et al. (2007). The experiment consisted of two phases. Prior to the first phase, *the vicarious learning phase*, participants were informed that they would initially watch a movie showing an experiment similar to the one they would themselves subsequently take part in. Participants were also informed that the person they were about to watch would receive electric shocks when one out of two visual stimuli was presented, and that the other stimulus would never be paired with a shock. Participants were asked to pay attention, but were given no instructions on where to look or about the specific CS–US contingencies.

An electrode was attached to the participant's arm before this phase of the experiment started. Participants were informed that this electrode would be used to administer electric shocks that would feel uncomfortable, but not painful. Importantly, participants never received any shocks, and none of the included participants had experience of electric shocks prior to taking part in the experiment, which ensured that the emotional learning was purely social/abstract in nature.

The next phase (*the test phase*) of the experiment started immediately after the vicarious learning phase. Participants were reminded of that they would themselves be presented with the same stimuli as the model had watched, and that the same stimulus would be paired with electric shocks. After this, each CS was presented, one at a time, in a pseudorandom order with a duration of 6000 ms, and an interstimulus interval of mean 13.7 s (sd = 1.12 s). Importantly, no actual shocks were administered. Afterwards, participants were debriefed, and asked to indicate whether they had believed that they would receive shocks. No participant expressed any doubt about this. As a manipulation check, participants were also asked to indicate how many shocks the model received, and to which stimulus the shocks were paired. Lastly, participants were asked to complete a set of questionnaires, see Section 2.4.3.

2.4. Data analysis

2.4.1. Definition of events

A CS+/− event was defined as the period between 0 and 5500 ms after onset of the CS. During reinforced trials shocks were administered to the model directly after this period. A vicarious shock event was defined as the period between 1000 and 3500 ms after administration of the shocks. Since the shocks produced brief visible movements in the models arm and face for a period of about 500 ms, this means that the included eye movements took place during a period without visible movement in the scene. The corresponding time periods after the onset of the CS− were used as baseline periods. Periods occurring during the 0–5500 ms time window after CS− onset are hereafter referred to as CS− events. Baseline periods corresponding to the vicarious shock events are referred to as no shock-events.

2.4.2. Eye tracking

A dispersion-based fixation filter was used to identify fixations in the raw data. The minimum duration was set to 100 ms, and the dispersion

diameter was set to cover approximately 1° of the visual field (see Blignaut, 2009 for a discussion about the choice of parameters). MATLAB scripts were used for the analyses. Gaze data were extracted during the time windows of the CS+/CS− and vicarious shock/no shock events. All data from an event was discarded if it contributed less than 1000 ms valid fixation time at the screen for the CS+/CS− events or less than 500 ms for the vicarious shock/no shock events. In total, more than 80% of trials were classified as valid. Only fixations initiated during the defined time windows were included in the analyses. If a fixation extended beyond the defined time window, this additional fixation time was excluded from further analysis. The following areas of interest (AOIs) were used in the analysis (see Fig. 1): 1) The model's face; 2) the model's arm, including the shock electrode; 3) the CS+/− that was presented to the model; and 4) the whole screen.

We computed the average fixation time within each AOI. This measure was defined as the total fixation duration inside each AOI divided by the number of valid events. Spearman correlations were calculated to analyze the relationships between gaze variables, the skin conductance responses and the trait measures. All gaze variables were normalized to the total fixation time at the screen before the correlations were computed.

2.4.3. Skin conductance responses (SCRs)

Skin conductance was analyzed off line with AcqKnowledge software (BIOPAC, CA). The raw skin conductance signal was low-passed filtered with a threshold of 1 Hz and high-passed filtered with a threshold of 0.01 Hz. The SCR amplitude was defined as the peak-to-peak value in microSiemens during the 500–4500 ms time window after the onset of each event.

Responses with amplitudes smaller than 0.02 mS were coded as 0. Raw data values were square root transformed to approach normal distribution. Skin conductance data were averaged over two blocks (early vs late) during both phases of the experiment to reduce inter-trial variability. Events 1–3 and 4–6 counted as early and late trials respectively during the test phase. For the vicarious learning phase, the first trial of each CS was excluded, because no differential learning could occur until the first CS-shock pairing was displayed.

The CR was operationalized as the average SCR amplitude to the CS+ minus the average SCR amplitude to the CS−, averaged over blocks. The UR was defined as the SCR to the following events during vicarious learning phase: the four vicarious shocks administered to the learning model minus the corresponding time intervals at the end of the CS− when no shocks were administered.

2.4.4. Trait empathy and autistic traits

The Empathy quotient (EQ; Lawrence et al., 2004) was used to measure trait empathy. The EQ is a 40 item self-report measure that includes items measuring both the perspective taking and emotional sides of empathy. Autistic traits were measures with the Autism Quotient (Baron-Cohen et al., 2001). The AQ includes 60 questions about behaviors and cognitions characteristic of autism spectrum disorder.

3. Results

3.1. Vicarious learning phase

3.1.1. Skin conductance

For the skin conductance data, a repeated measures ANOVA with CS(+/−) and block (early block/late block) as within subjects factors revealed a main effect of CS ($F(1,32) = 21.67$; $p < .001$), reflecting higher SCR amplitude to the CS+ ($M = .56$; $sd = .45$) as compared to the CS− ($M = 35$; $sd = .30$). This demonstrates that participants showed a CR during the vicarious learning phase. In addition, a repeated measures ANOVA with event type (vicarious shock vs. no shock) and time (events 1–4) as within subjects factors revealed a main effect of event type ($F(1,33) = 8.02$; $p < .05$), reflecting larger SCR amplitude to vicarious shocks ($M = 1.02$; $sd = .68$) than during no shock events ($M = .51$; $sd = .41$).

3.1.2. Eye gaze

Average fixation times at the face, arm and CS AOIs during CS+/CS− events are displayed in Fig. 2A. An ANOVA with CS(+/−) and region as factors revealed a main effect of region ($F(1.46,25) = 9.24$; $p < .01$, *Greenhouse–Geisser correction*) and a CS × region interaction, ($F(1.62,27) = 4.70$; $p < .05$), but no main effect of CS. Post hoc tests revealed that the CS × region interaction was driven by longer fixation times to the CS AOI during CS− ($M = 978$ ms; $sd = 888$ ms) than during CS+ events ($M = 815$ ms; $sd = 811$; $t(26) = 2{,}12$; $p < .05$). In addition, participants looked longer at the model's face during CS+ ($M = 1110$ ms; $sd = 888$) than CS− events ($M = 997$ ms; $sd = 859$). This difference approached statistical significance ($t(26) = 1.93$; $p = .06$). Collapsing data over trials, post hoc comparisons showed that the main effect of AOI was driven by longer fixation time at the CS than at the arm ($t(26) = 4.64$; $p < .001$), and longer fixation time at the face than the arm ($t(26) = 4.109$; $p < .001$). No differences in fixation time emerged between the face and arm area ($p > .05$).

Fig. 2B shows average fixation times to the face, arm and stimulus AOIs during vicarious shock and no-shock trials. An event (vicarious shock/no shock) × region repeated measure ANOVA showed a main effect of region, ($F(2,25) = 15.87$; $p < .001$), and a significant interaction between event type and region ($F(2,25) = 7.89$; $p < .01$). Post hoc tests showed that the event type × region interaction was driven by longer fixation time at the face than the CS AOI ($t(26) = 2.30$; $p < .05$) during vicarious shock events, whereas no reliable difference between these regions was found during no shock events ($p > .05$).

3.1.3. Trait measures

A significant positive correlation was found between EQ scores and fixation time at the CS AOI during CS+ events ($rs(26) = .48$; $p < .05$), indicating that participants high in trait empathy looked longer at the CS+ that predicted aversive treatment to the model (see Fig. 3B). AQ scores were positively related to the strength of the UR ($rs(32) = .49$; $p < .01$). In contrast, fixation time to the face, arm or CS AOI was not related to the strength of the UR ($ps > .05$).

3.2. Test phase

3.2.1. Skin conductance

For the skin conductance data, a repeated measures ANOVA with CS(+/−) and block (early/late) demonstrated a main effect of CS ($F(1,32) = 15.81$; $p < .001$), reflecting higher SCR amplitude to the CS+ ($M = 1.42$; $sd = .70$) than to the CS− ($M = .97$; $sd = .69$). This shows that the CR persisted into the test phase. A main effect of block was also found ($F(1,32) = 30.82$; $p < .001$), with average SCR decreasing over time.

3.2.2. Eye gaze

In order to examine the relationship between gaze pattern during the vicarious learning phase and skin conductance during the test phase, we calculated the proportion of total fixation time directed at the CS AOI during CS+ events, and found that this measure positively correlated with the strength of the CR during the subsequent test phase ($rs(26) = .40$; $p < .05$). This correlation is shown in Fig. 3A. In contrast, no relationship was found between the proportion of fixation time at the model's face and the CR.

3.2.3. Trait measures

In addition, EQ scores were positively related to the CR ($rs(33) = .48$; $p < .01$). Since the CR is dependent on the strength of responses to both the CS+ and the CS−, both of these factors could potentially explain

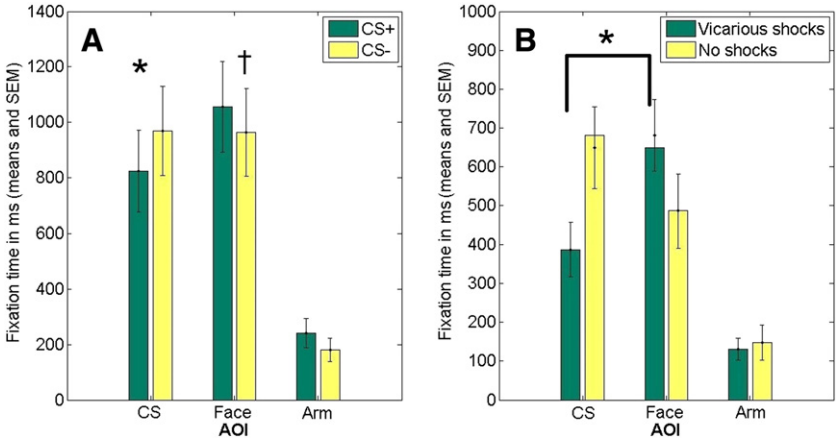

Fig. 2. Average fixation time in each AOI. (*$p < .05$; †$p = .06$).

the relationship between trait empathy, fixation time at the model's face, and the CR. In an exploratory analysis, we correlated the two former variables with the average SCR amplitude to the CS+ and CS− during the test phase separately. SCR amplitude to the CS− was negatively correlated with both EQ scores ($rs(26) = -.39$; $p < .05$) and fixation time to the CS+ ($rs(26) = .44$; $p < .05$). In contrast, neither EQ, nor fixation time at the CS+, were correlated with SCR amplitude to the CS+ ($ps > .50$). AQ scores did not predict the strength of the CR during the test phase ($p > .05$).

4. Summary and discussion

We aimed at examining eye movements during the acquisition and expression of vicarious fear learning. We hypothesized that participants' eye movements would differ depending on whether the CS+ or CS− was displayed to the model. We also expected that participants' gaze patterns would be related to the UR and predictive of the subsequently expressed CR. Finally, we expected that eye movements would be related to autistic traits and trait empathy. Our results can be summarized in terms of five key findings.

First, we found evidence of vicarious fear learning both during the observation of the punished model (vicarious learning phase), and at a later time-point in the absence of the model. This supports previous studies on vicarious or observational fear learning (Olsson and Phelps, 2007). Our results also showed that participants displayed a consistent UR to vicarious shocks. This response is likely to reflect empathic appraisals of the model's presumed pain, learning and expectancies about the CS–US association.

Second, as predicted, we demonstrated that participants' eye movements differed depending on whether the CS that was presented to the model was predictive of shock or not. More specifically, we found that when the CS+ as compared to the CS− was present, participants looked more at the face of the model and less at the CS AOI. The same gaze pattern characterized the intervals directly after the vicarious shocks. Importantly, the model exhibited a neutral facial expression and made no movements except briefly when the actual shocks were administered. This suggests that the differences in eye movements after the shock were not accounted for by low-level visual properties of the scene or its intrinsic emotional value. Instead, we speculate that these differences reflected the differential salience of the scene resulting from social learning, the search for information predictive of the US administration, and, possibly, from attributions of mental states (thoughts and feelings) to the model. In sum, our measures of spontaneous eye movements showed that attention was enhanced to emotionally salient and threat relevant cues, including those informative of the CS–US contingency and the quality of the US. This is consistent with previous studies that have shown different patterns of eye movements (Calvo and Lang, 2004; Hunnius et al., 2011; Nummenmaa et al., 2006), and perceptual sensitivity (Åhs et al., 2013; Phelps et al., 2006) to threat-related as compared to non-threat related visual stimuli. Our results demonstrate

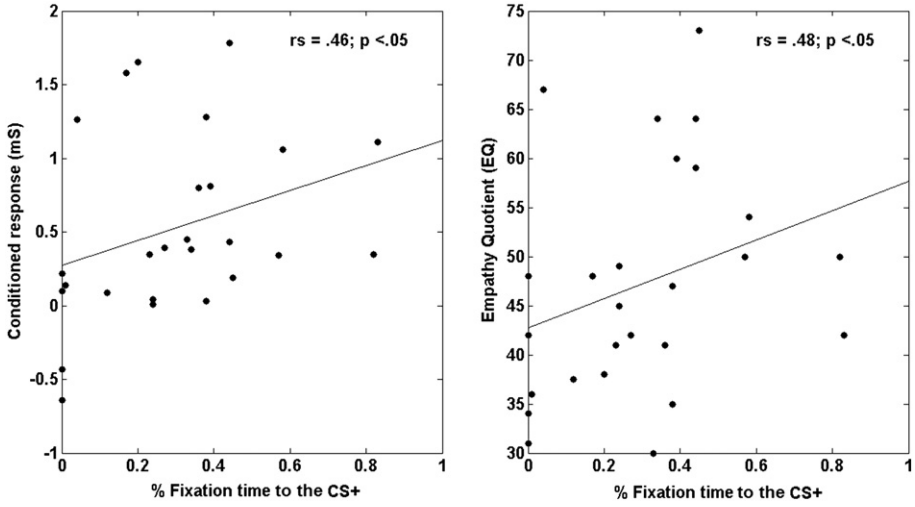

Fig. 3. A) Relationship between the conditioned response (CR) and the proportion of fixation time at the CS+ during the vicarious learning phase. CR values are shown in mS (square-root transformed values). B) Relationship between Empathy Quotient (EQ) scores and % fixation time at the CS+ during the vicarious learning phase.

that this is also true of stimuli in naturalistic visual scenes that have become threat relevant through social learning. This adds support to research showing that eye movements and attention to the human face is important for discriminatory learning about aspects of the environment through social observation (Meltzoff et al., 2009; Frith and Frith, 2007). Our results that the presence of the CS+ resulted in increased fixation time at the model's face support a theoretical model of vicarious fear learning in which facial or bodily expressions of distress in a model can serve as a powerful 'social' US, similar to the role of a directly experienced US in traditional Pavlovian conditioning procedures (Askew and Field, 2007; Mineka et al., 1984). Interestingly, this was shown even in the absence of strong facial expressions of distress, further supporting the suggestion that empathic appraisals of the punished model's experiences play an important role (Olsson and Ochsner, 2008; Olsson et al., submitted for publication).

Third, and further strengthening the predicted link between eye movements and vicarious fear learning, we showed that the proportion of fixation time at the CS+ predicted the strength of the subsequently expressed CR in the absence of the model during the later test phase. Additional analyses demonstrated that this relationship was driven by reduced SCR amplitude to the CS− rather than by increased SCR amplitude to the CS+, underscoring the role of attention in safety learning (i.e., learning the value of the 'safe' CS−).

Our fourth main finding was that trait empathy was positively related to both the strength of the CR and to the proportion of fixation time directed to the CS AOI. This supports the notion that an underlying mechanism of trait empathy is enhanced attention to socially salient aspects of the environment (Hofelich and Preston, 2012).

A somewhat surprising finding is that although attention to the models' face increased during CS+ events, fixation time at this area did not predict the strength of the CR. Instead, fixation time at the CS AOI was predicted stronger learning despite the fact that participant's actually looked less at this area during CS+ presentations. This is in line with a previous study that demonstrated enhanced visual attention to a CS+ after Pavlovian fear conditioning (Eippert et al., 2012). (The relationship between trait empathy and the strength of the CR is strengthening the assumption that the ability to process social–cognitive and emotional information is important in determining the outcome of vicarious learning. A similar result was demonstrated in a study describing that individual differences in trait empathy strengthened the positive effect of empathy appraisals of the model's pain during vicarious fear learning (Olsson et al., *submitted*).)

Fifth and finally, we found that participants high in autistic traits showed a stronger UR. In contrast to trait empathy, and contrary to our predictions, no association was found between autistic traits and the CR. These results are partly inconsistent with the results from Miu et al. (2012) that demonstrated a stronger CR in people with high levels of autistic traits. This inconsistency may be related to differences in both data analysis and the sample. We computed linear correlations between AQ scores and SCR variables, whereas Miu and colleagues compared two groups created post hoc on the basis of their AQ scores. Only four of the participants in the present study had AQ scores above the cutoff point (>21), which was the inclusion criterion for the group with high AQ score in the study by Miu and colleagues. Another interesting possibility is that the relationship between autistic traits and vicarious learning of fear is not linear, but depends on state arousal. Previous studies have found evidence of atypical arousal regulation in participants with ASD, which may relate to variability in emotional and cognitive functions (Kleberg, accepted for publication; Pfaff et al., 2011).

A limitation of our study is its correlational nature. Although our results suggest that there may be a functional link between vicarious fear learning and eye movements, it is not possible to draw any conclusions about direct causal relationships. Future studies should examine the role of eye movements in vicarious learning further, for instance by preventing eye movements during the vicarious learning phase. If reduced fear learning can be demonstrated when participants are required to fixate at a central part of the scene, this would support a causal role of eye movements. Similarly, experimental manipulations of empathic appraisals are needed to better understand the relationship between empathy and vicarious fear learning. It should also be noted that our sample was limited in its range of autistic traits. This may have resulted in a floor effect for this measure.

To sum up, our study presents the first attempt to examine the mechanisms of vicarious fear learning by characterizing the patterns of eye movements both during the vicarious acquisition of fear, and during the subsequent expression of the acquired learning in the absence of the model. Taken together, we show that the temporal and spatial allocation of fixations to the learning model and the CS are related to SCRs during vicarious learning. In particular, fixating longer at the CS+ was positively predictive of subsequent autonomic indices of learning. We also show that the presence of the CS+ resulted in increased fixation time at the model's face.

In addition, we show that individual differences in trait empathy were related to both fixation time at the CS+ and to the strength of the subsequent expressed learning. In addition, autistic traits are related to both the autonomic responses to the learning model's distress. Our results point in several directions for future research. A dysfunctional social learning system might be the origin of both exaggerated fear and anxiety, as manifested in anxiety disorders, and in the inability to develop adaptive associations between emotionally important stimuli, such as in autism spectrum disorders. Therefore, an important step for future research will be to investigate these processes in clinical groups.

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References

Åhs, F., Miller, S.S., Gordon, A.R., Lundström, J.N., 2013. Aversive learning increases sensory detection sensitivity. Biol. Psychol. 92 (2), 135–141.
Askew, C., Field, A.P., 2007. Vicarious learning and the development of fears in childhood. Behav. Res. Ther. 45 (11), 2616–2627.
Bandura, A., Rosenthal, T.L., 1966. Vicarious classical conditioning as a function of arousal level. J. Pers. Soc. Psychol. 3 (1), 54.
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. J. Autism Dev. Disord. 31 (1), 5–17.
Berger, S.M., 1962. Conditioning through vicarious instigation. Psychol. Rev. 69 (5), 450.
Bernhardt, B.C., Singer, T., 2012. The neural basis of empathy. Annu. Rev. Neurosci. 35, 1–23.
Bernier, R., Dawson, G., Panagiotides, H., Webb, S., 2005. Individuals with autism spectrum disorder show normal responses to a fear potential startle paradigm. J. Autism Dev. Disord. 35 (5), 575–583.
Blair, R., 2003. Facial expressions, their communicatory functions and neurounctions and neurot no. Philos. Trans. R. Soc. B 358 (1431), 561–572.
Blair, R., 2008. Fine cuts of empathy and the amygdala: dissociable deficits in psychopathy and autism. Q. J. Exp. Psychol. 61 (1), 157–170.
Blignaut, P., 2009. Fixation identification: the optimum threshold for a dispersion algorithm. Atten. Percept. Psychophys. 71 (4), 881–895.
Calvo, M.G., Lang, P.J., 2004. Gaze patterns when looking at emotional pictures: Motivationally biased attention. Motiv. Emot. 28 (3), 221–243.
Dalton, K.M., Nacewicz, B.M., Alexander, A.L., Davidson, R.J., 2007. Gaze-fixation, brain activation, and amygdala volume in unaffected siblings of individuals with autism. Biol. Psychiatry 61 (4), 512–520.
Debiec, J., Sullivan, R.M., 2014. Intergenerational transmission of emotional trauma through amygdala-dependent mother-to-infant transfer of specific fear. Proc. Natl. Acad. Sci. U. S. A. 201316740.

Eippert, F., Gamer, M., Büippe, C., 2012. Neurobiological mechanisms underlying the blocking effect in aversive learning. J. Neurosci. 32 (38), 13164–13176.
Falck-Ytter, T., Gredebäck, G., von Hofsten, C., 2006. Infants predict other people's action goals. Nat. Neurosci. 9 (7), 878–879.
Findlay, J.M., Gilchrist, I.D., 2003. Active Vision: The Psychology of Looking and Seeing. Oxford University Press.
Frith, C.D., Frith, U., 2007. Social cognition in humans. Curr. Biol. 17 (16), R724–R732.
Gaigg, S.B., Bowler, D.M., 2007. Differential fear conditioning in Asperger's syndrome: implications for an amygdala theory of autism. Neuropsychologia 45 (9), 2125–2134.
Golkar, A., Castro, V., Olsson, A., 2015. Social learning of fear and safety is determined by the demonstrator's racial group. Biol. Lett. 11 (1), 20140817.
Goubert, L., Vlaeyen, J.W., Crombez, G., Craig, K.D., 2011. Learning about pain from others: an observational learning account. J. Pain 12 (2), 167–174.
Green, M., Williams, L., Davidson, D., 2003. In the face of danger: specific viewing strategies for facial expressions of threat? Cogn. Emot. 17 (5), 779–786.
Guillon, Q., Hadjikhani, N., Baduel, S., Rogé, B., 2014. Visual social attention in autism spectrum disorder: insights from eye tracking studies. Neurosci. Biobehav. Rev. 42, 279–297.
Helsen, K., Goubert, L., Vlaeyen, J.W., 2013. Observational learning and pain-related fear: exploring contingency learning in an experimental study using colored warm water immersions. J. Pain 14 (7), 676–688.
Henderson, J.M., Williams, C.C., Falk, R.J., 2005. Eye movements are functional during face learning. Mem. Cogn. 33 (1), 98–106.
Hofelich, A.J., Preston, S.D., 2012. The meaning in empathy: Distinguishing conceptual encoding from facial mimicry, trait empathy, and attention to emotion. Cogn. Emot. 26 (1), 119–128.
Hunnius, S., de Wit, T.C., Vrins, S., von Hofsten, C., 2011. Facing threat: Infants' and adults' visual scanning of faces with neutral, happy, sad, angry, and fearful emotional expressions. Cogn. Emot. 25 (2), 193–205.
Hygge, S., Öhman, A., 1978. Modeling processes in the acquisition of fears: vicarious electrodermal conditioning to fear-relevant stimuli. J. Pers. Soc. Psychol. 36 (3), 271.
Jeon, D., Kim, S., Chetana, M., Jo, D., Ruley, H.E., Lin, S.-Y., Shin, H.-S., 2010. Observational fear learning involves affective pain system and Cav1. 2 Ca^{2+} channels in ACC. Nat. Neurosci. 13 (4), 482–488.
Kleberg, J.L., 2014. Resting state arousal and brain activity in Autism Spectrum Disorder. J. Neurophysiol. (jn. 00292.02014, accepted for publication).
Klin, A., Jones, W., Schultz, R., Volkmar, F., Cohen, D., 2002. Visual fixation patterns during viewing of naturalistic social situations as predictors of social competence in individuals with autism. Arch. Gen. Psychiatry 59 (9), 809–816.
Lawrence, E., Shaw, P., Baker, D., Baron-Cohen, S., David, A., 2004. Measuring empathy: reliability and validity of the Empathy Quotient. Psychol. Med. 34 (05), 911–920.
LeDoux, J., 2012. Rethinking the emotional brain. Neuron 73 (4), 653–676.
Meffert, H., Brislin, S.J., White, S.F., Blair, J.R., 2014. Prediction errors to emotional expressions: the roles of the amygdala in social referencing. Soc. Cogn. Affect. Neurosci. 10 (4), 537–544.
Meltzoff, A.N., Kuhl, P.K., Movellan, J., Sejnowski, T.J., 2009. Foundations for a new science of learning. Science 325 (5938), 284–288.
Mineka, S., Cook, M., 1993. Mechanisms involved in the observational conditioning of fear. J. Exp. Psychol. Gen. 122 (1), 23.
Mineka, S., Davidson, M., Cook, M., Keir, R., 1984. Observational conditioning of snake fear in rhesus monkeys. J. Abnorm. Psychol. 93 (4), 355.
Miu, A.C., Pan, S.E., Avram, J., 2012. Emotional face processing in neurotypicals with autistic traits: implications for the broad autism phenotype. Psychiatry Res. 198 (3), 489–494.
Nummenmaa, L., Hyöum, J., Calvo, M.G., 2006. Eye movement assessment of selective attentional capture by emotional pictures. Emotion 6 (2), 257.
Olsson, A., Phelps, E.A., 2004. Learned fear of "unseen" faces after Pavlovian, observational, and instructed fear. Psychol. Sci. 15 (12), 822–828.
Olsson, A., Phelps, E.A., 2007. Social learning of fear. Nat. Neurosci. 10 (9), 1095–1102.
Olsson, A., Ochsner, K.N., 2008. The role of social cognition in emotion. Trends Cogn. Sci. 12 (2), 65–71.
Olsson, A., Nearing, K.I., Phelps, E.A., 2007. Learning fears by observing others: the neural systems of social fear transmission. Soc. Cogn. Affect. Neurosci. 2 (1), 3–11.
Olsson, A., McMahon, K., Papenberg, G., Zaki, J., Bolger, N., Ochsner, K.N., 2015. Vicarious Fear Learning depends on Empathic Appraisals and Trait Empathy (submitted for publication).
Pfaff, D.W., Rapin, I., Goldman, S., 2011. Male predominance in autism: neuroendocrine influences on arousal and social anxiety. Autism Res. 4 (3), 163–176.
Phelps, E.A., LeDoux, J.E., 2005. Contributions of the amygdala to emotion processing: from animal models to human behavior. Neuron 48 (2), 175–187.
Phelps, E.A., O'Connor, K.J., Gatenby, J.C., Gore, J.C., Grillon, C., Davis, M., 2001. Activation of the left amygdala to a cognitive representation of fear. Nat. Neurosci. 4 (4), 437–441.
Phelps, E.A., Ling, S., Carrasco, M., 2006. Emotion facilitates perception and potentiates the perceptual benefits of attention. Psychol. Sci. 17 (4), 292–299.
Preston, S.D., De Waal, F., 2002. Empathy: its ultimate and proximate bases. Behav. Brain Sci. 25 (01), 1–20.
Rachman, S., 1977. The conditioning theory of fear acquisition: a critical examination. Behav. Res. Ther. 15 (5), 375–387.
Rendell, L., Boyd, R., Cownden, D., Enquist, M., Eriksson, K., Feldman, M.W., Laland, K.N., 2010. Why copy others? Insights from the social learning strategies tournament. Science 328 (5975), 208–213.
Ronald, A., Hoekstra, R.A., 2011. Autism spectrum disorders and autistic traits: a decade of new twin studies. Am. J. Med. Genet. B 156 (3), 255–274.
South, M., Larson, M.J., White, S.E., Dana, J., Crowley, M.J., 2011. Better fear conditioning is associated with reduced symptom severity in autism spectrum disorders. Autism Res. 4 (6), 412–421.
Tomasello, M., 2009. The Cultural Origins of Human Cognition. Harvard University Press.