



Original Articles

Human body motion captures visual attention and elicits pupillary dilation

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ARTICLE INFO

Keywords:

Biological motion
 Social reward
 Social motivation
 Pupillometry
 Eye-tracking
 Attentional disengagement

ABSTRACT

The social motivation theory proposes that individuals naturally orient their attention to the social world. Research has documented the rewarding value of social stimuli, such as biological motion, to typically developed individuals. Here, we used complementary eye tracking measures to investigate how social motion cues affect attention and arousal. Specifically, we examined whether viewing the human body moving naturally versus mechanically leads to greater attentional engagement and changes in autonomic arousal (as assessed by pupil size measures). Participants completed an attentional disengagement task in two independent experiments, while pupillary responses were recorded. We found that natural, human-like motion produced greater increases in attention and arousal than mechanical motion, whether the moving agent was human or not. These findings contribute an important piece to our understanding of social motivation by demonstrating that human motion is a key social stimulus that engages visual attention and induces autonomic arousal in the viewer.

1. Introduction

From birth, humans show a strong preference for social stimuli, termed ‘social motivation’ (Chevallier, Kohls, Troiani, Brodtkin, & Schultz, 2012; Dawson, Meltzoff, Osterling, Rinaldi, & Brown, 1998; Fletcher-Watson, Findlay, Leekam, & Benson, 2008), as demonstrated by our reliable attentional preferences for biologically relevant stimuli including faces, voices, and the human body (Alegria & Noirot, 1978; Fox & McDaniel, 1982; Valenza, Simion, Cassia, & Umiltà, 1996). Social stimuli, such as human faces and bodies, provide valuable information about an observed individual, including their age, gender, race, identity, emotions and intentions. Reduced social motivation is suggested to cause deficits in social reward processing, which might have negative downstream consequences for social cognition in conditions such as Autism Spectrum Condition (ASC¹; Chevallier et al., 2012).

The Social Motivation Theory (Chevallier et al., 2012) proposes three tiers of social motivation: social orienting, social maintaining, and social seeking and liking. This theory suggests that we possess a set of behavioural dispositions that guide us to preferentially orient our attention to the social world (social orienting/attention), behave in ways that allow us to develop, strengthen, and maintain our social

relationships (social maintaining), and to seek social interaction and take pleasure in our relationships (social seeking and liking/reward). The present study focuses on the social orienting and social reward aspects of social motivation.

Our attention is captured and engaged by biologically relevant stimuli more quickly than other types of non-social stimuli (Fletcher-Watson et al., 2008; Lavie, Ro, & Russell, 2003; Purcell & Stewart, 1988). This attentional bias to social stimuli is demonstrated by our ability to quickly detect social stimuli (Fletcher-Watson et al., 2008; Purcell & Stewart, 1988), and also, our slow disengagement from social stimuli and towards non-social stimuli (Lavie et al., 2003; Senju & Hasegawa, 2005).

In 2005, Senju and Hasegawa provided further evidence for social attention (Senju & Hasegawa, 2005). They used an attentional disengagement task to demonstrate that typically developed (TD) participants detect peripheral targets more slowly when viewing facial images displaying direct versus averted gaze. These slower reactions to targets could be due to increased attentional dwell time given to facial stimuli that convey biologically important information (Fox & McDaniel, 1982). Individuals with ASC, however, show no differences in attentional dwell time when shown faces or non-social objects (Kikuchi,

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¹ We refer throughout to individuals with an Autism Spectrum Condition (ASC), but we acknowledge and respect that some individuals in the autistic community prefer to be referred to as ‘autistic individuals’ (Kenny et al., 2016). However, for clarity and consistency with the prior literature in this domain, we use individuals with ASC throughout.

Senju, Hasegawa, Tojo, & Osanai, 2013). Other studies have reported preferential attention given to biological motion (motion patterns associated with living organisms) in newborns, which is crucial for facilitating adaptive interactions across phylogeny (Bardi, Regolin, & Simion, 2011). Evidence also shows that TD infants naturally attend to biological motion (Fox & McDaniel, 1982), and that this behaviour is impaired in infants with ASC (Klin, Lin, Gorrindo, Ramsay, & Jones, 2009).

One reason our attention is captured easily by social stimuli is because of their potentially beneficial or rewarding nature (Chevallier et al., 2012; Dubey, Ropar, & Hamilton, 2015; Haffey, Press, O'Connell, & Chakrabarti, 2013; Sims, Van Reekum, Johnstone, & Chakrabarti, 2012; Williams & Cross, 2018). Recent studies have used effort tasks, where participants choose to exert effort to view their preferred stimuli, to better understand and measure the reward value of social stimuli (Dubey et al., 2015; Williams & Cross, 2018). These studies report that TD individuals exert more effort to view videos of faces with a direct gaze, compared to non-social objects (Dubey et al., 2015), and to view videos of humans moving naturally compared to mechanically, further reinforcing the reward value of socially relevant stimuli (Williams & Cross, 2018). Participants reporting more autistic traits or with ASC diagnoses showed a reduced preference for social stimuli across both studies.

While explicit preference tasks provide a useful means to investigate social reward, another promising approach involves measuring pupil dilation to assess implicit and automatic reward processing (Murphy, Robertson, Balsters, & O'Connell, 2011; Sepeta et al., 2012). Pupil size not only changes in response to light, but it is also linked to arousal level, attention, processing load, thoughts, and emotions (Beatty, 1982; Goldwater, 1972; Hess & Polt, 1964; Kahneman & Beatty, 1966; Sepeta et al., 2012; Unsworth & Robison, 2016). Research has shown pupil dilation in response to arousing stimuli (with either positive or negative valence; Bradley, Miccoli, Escrig, & Lang, 2008), and rewarding stimuli, such as those that are sexually arousing compared to not sexually arousing (Hess, Seltzer, & Shlien, 1965; Rieger & Savin-Williams, 2012), or when anticipating large rewards compared to smaller rewards (Bijleveld, Custers, & Aarts, 2009; Chae et al., 2008). For example, smoking-related cues produce pupillary dilations in smokers but not non-smokers (Chae et al., 2008); these cues also activate reward-related brain regions, such as the ventral striatum (Wang et al., 2007), suggesting that pupil dilation can act as a proxy for reward processing.

Sepeta et al. (2012) used pupillary reactions to measure autonomic responses (as a proxy for reward) of children with and without ASD when viewing facial images. They found TD children showed greater pupil dilation when viewing images of happy faces showing direct versus averted gaze. This association with gaze direction was absent among children with ASC. Thus, increased pupil diameter among TD children when directly viewing happy faces might reflect the intrinsic reward value of a face looking directly at the observer. Indeed, the rewarding value of faces to TD participants is well established (Dubey et al., 2015; Hayden, Parikh, Deaner, & Platt, 2007; Shore & Heerey, 2011). The absence of increased pupil diameter among children with ASC suggests they have reduced sensitivity to the reward value of this stimulus.

It is currently unclear whether other salient social cues, such as biological human body motion, engage attention more than non-social cues do. We also do not know the extent to which socially relevant body form and body motion cues might induce autonomic responses in participants due to their rewarding value.

Here, we assess the social attention aspect of social motivation, by testing the hypothesis that attention is engaged more by naturalistic than by mechanistic motion, and by a human body compared to a non-human agent, using two different eye-tracking experiments performed with TD individuals. We measured the time participants took to disengage attention from different video stimuli and attend to peripheral targets, using saccades as a measure of attentional disengagement in

Experiment 1, and a button-press response measure in Experiment 2. We hypothesised that, due to the social importance of biological motion and its potentially rewarding or beneficial nature, participants should show the longest attentional dwell time for natural motion performed by a human body (shown by delayed saccadic response times in Experiment 1, and by delayed behavioural response times in Experiment 2). Although our main objective was to investigate participants' engagement with natural compared to machine-like motion, our experimental design also enabled us to investigate whether it is the social nature of the agent type (human or non-human) or the motion type (natural or mechanical) that individuals find most engaging. We also predicted that individuals reporting more autistic traits would show less pronounced differences in attentional dwell time for videos of natural compared to mechanistic motion, whereas those reporting fewer autistic traits would be slower to disengage from natural than mechanistic motion.

Using a measure of autonomic arousal as a proxy for the social reward aspect of social motivation, we investigated whether differences in pupil size emerge while participants view the different video categories to test the hypothesis that participants would show greater pupil dilation when viewing videos of human bodies moving naturally compared to other videos. We also examined the relationship between autistic traits and pupil size when viewing the different categories of videos, hypothesising that individuals reporting more autistic traits would show less of an increase in pupil size when viewing human bodies moving naturally.

2. Experiment 1

Previous studies of attentional disengagement have primarily measured attentional dwell time via button responses to peripheral targets. However, measuring attentional disengagement by saccades is thought to highlight more subtle differences in response times (Azarian, Esser, & Peterson, 2016; Belopolsky, Devue, & Theeuwes, 2011). In light of this, participants in Experiment 1 completed an attentional disengagement task where they watched a video until a peripheral target appeared, at which time they were asked to saccade toward the peripheral target.

2.1. Materials and method

Consistent with recent proposals (Simmons, Nelson, & Simonsohn, 2011, 2012), we report how we determined our sample size, all data exclusions, all manipulations and all measures in the study. In addition, following open science initiatives (e.g., Munafò et al., 2017), the de-identified data sets, stimuli and analysis code associated with this study are freely available online (<https://osf.io/pdcnr/>). By making the data available, we enable and encourage others to pursue tests of alternative hypotheses, as well as more exploratory analyses.

2.1.1. Participants

Fifty-one participants were recruited from the local community or from Bangor University's student participant panel. Data from one participant were excluded due to a technical issue that resulted in data from a quarter of the trials not being recorded, and one further participant was excluded due to having an Autism Quotient score more than 2 standard deviations away from the mean, leaving a final sample for data analysis of 49 participants (35 females; $M_{\text{age}} = 23.80$, $SD_{\text{age}} = 4.79$). Participants were reimbursed £7 per hour or were given course credits for their time. The sample size was determined prior to data collection using the G*Power calculator (Faul, Erdfelder, Buchner, & Lang, 2009; Faul, Erdfelder, Lang, & Buchner, 2007), which enabled us to detect medium-to-large effect sizes with 80% power. However, this sample was determined for analyses using repeated-measures ANOVA rather than mixed-effects modelling, due to the complexity of conducting power analyses for experiments employing mixed-effects models (Kain, Bolker, & McCoy, 2015). All participants had normal or

corrected-to-normal vision, provided written informed consent, and Bangor University's School of Psychology Research Ethics Committee granted ethical approval (Ethics Approval Code: 2015-15400), following procedures in accordance with the Declaration of Helsinki.

2.1.2. Stimuli

Four categories of video stimuli developed for a previous study (Williams & Cross, 2018) were used. The first and second category of videos featured a human actor performing Natural Human Motion (movements such as moving arms and legs from side to side smoothly) and Machine-Like Motion (movements such as moving arms and legs from side to side rigidly). These two stimulus categories included 10 unique videos each, and are henceforth referred to as 'Human Body Natural Motion' and 'Human Body Machine-Like Motion', respectively. Human Body Natural Motion videos were created as a proxy for biological motion, and Human Body Machine-Like Motion videos were created as a proxy for non-biological motion (for further discussion of the utility of this approach, please see Williams & Cross, 2018). Videos were captured using the Kinect platform (Microsoft), where a video stream and the agent motion structure were extracted. From these video recordings, five computer generated image (CGI) videos featuring a non-human control agent "performing" Natural Motion and five "performing" Machine-Like Motion were created using the same motion as the human ones; these are referred to as Control Agent Natural Motion and Control Agent Machine-Like Motion (Fig. 1). Participants saw each stimulus for at least 2.5 s (i.e., the combination of the shortest stimulus onset asynchronies (SOA), plus saccade latency). The moving agents appeared without heads, as facial information could be a potential confound in the study. For more details about how the stimulus sets were created, see Williams and Cross (2018).

A static target was placed onto the torso of both the human and control agents, and the torso region remained stationary so that participants had a stable point in the video to fixate. This manipulation also allowed for more controlled pupil measurements as pupil size can change with gaze position and eye movements (Brisson, Mainville, Mailloux, Beaulieu, Serres, & Sirois, 2013).

Fluctuations in pupil size also occur as a result of changes in luminance in stimuli (Mathôt, 2018; Woodhouse, 1975). This pupillary light reflex has been suggested to be one of the main confounds in cognitive pupillometry (Sirois & Brisson, 2014; Woodhouse, 1975).

Thus, we verified that the luminance levels of both motion categories did not significantly differ from each other. Although the luminance differed across the agent types (human vs. control), importantly, no differences in luminance were present between the motion categories (see Supplementary Materials for full luminance analysis), thus confirming that any changes between motion categories were not due to low-level differences in luminance between the stimuli. The videos fell into a 2×2 factorial design, with Agent Type (human body or control) and Motion (natural or machine-like) as factors.

2.1.3. Apparatus

Saccadic eye-movements and pupil size were recorded from only the right eye of participants, using an EyeLink 1000 desk-mounted eye-tracker (SR Research Ltd., Mississauga, ON, Canada), which sampled at 1000 Hz. Pupil diameter was measured in arbitrary units as recorded by the eye-tracker. Participants sat in a comfortable chair, with a pillow to limit head movements, in a dimly lit room with no windows. Videos were presented in the center of a screen at a viewing distance of 100 cm. Target dots were displayed either to the left or to the right of the main video. All stimuli were presented on a 27-inch monitor with a resolution of 1080×1920 (60 Hz refresh rate). The stimuli subtended at the maximum 14° by 14° of visual angle and were presented on a white background. The experiment was presented using Experiment Builder (version 1.10.1630; SR Research Ltd, 2004).

2.1.4. Procedure

The experiment began with a 9-point calibration of the eye-tracker followed by a validation stage. Recalibrations took place after each experimental block, and when needed (e.g., if a participant's head moved too much, or someone wanted a break mid-block). Participants completed 1 practice block of 12 trials, followed by 4 experimental blocks of 60 trials. The trials within these blocks were randomised and included a combination of the four stimulus types. Participants were given the opportunity to take a break after each block.

Each trial began with a central fixation cross to perform a drift correction, followed by a video stimulus. Participants were required to maintain fixation on the circular target on the torso of the agent in the video. A target dot appeared in a non-predictive fashion to the left or to the right of the stimulus, either 2500 ms or 3000 ms after video onset (Fig. 2). These 2 SOAs were chosen to give the participant enough time

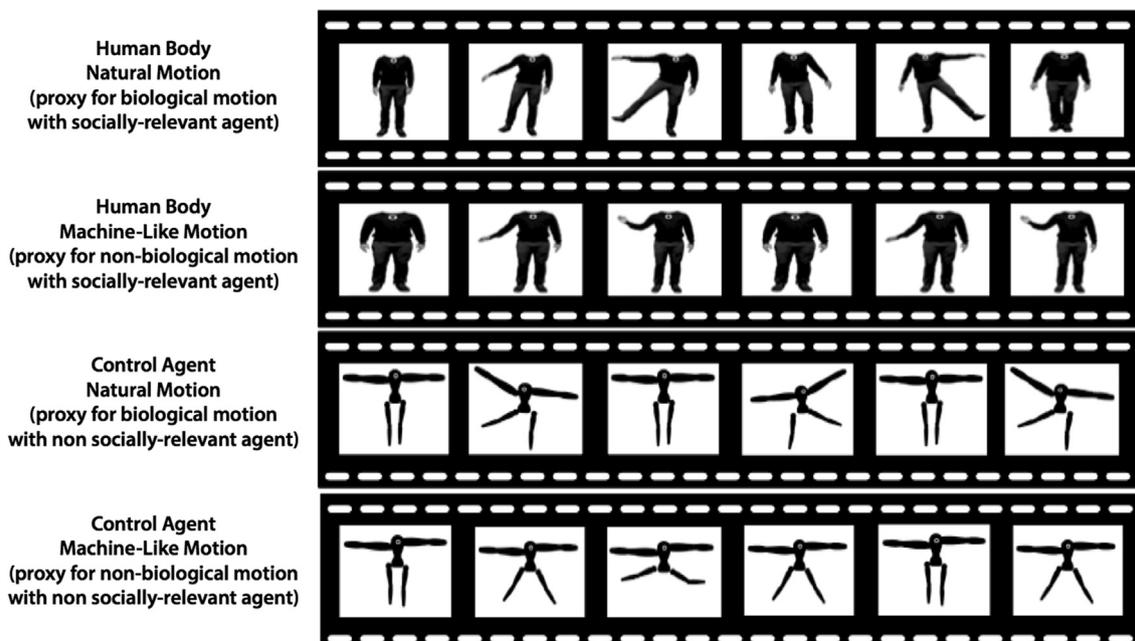


Fig. 1. Example video stills from the four stimulus categories.

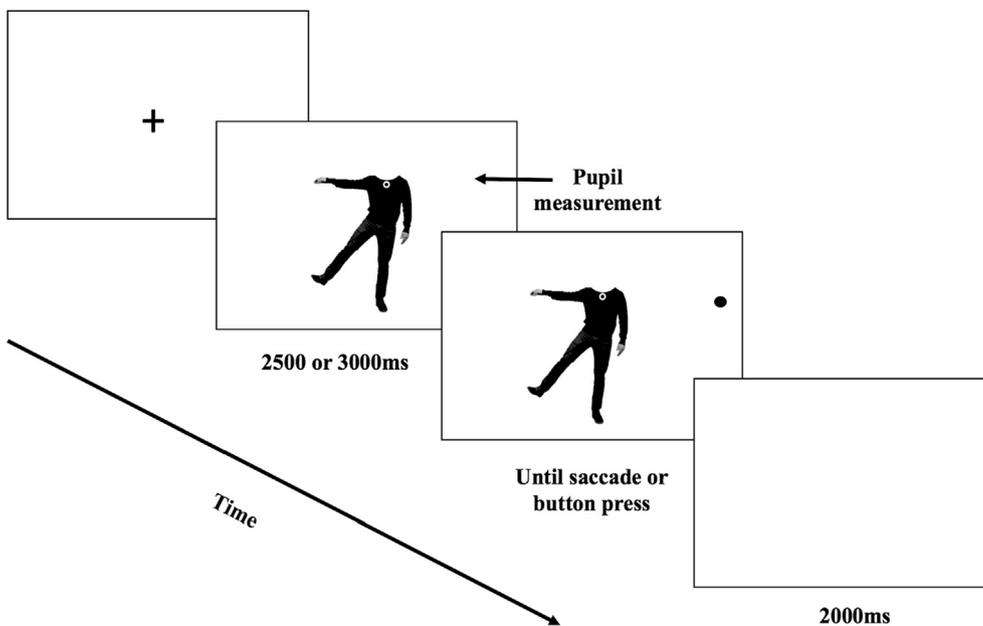


Fig. 2. Example of a trial with a video of a human body performing natural motion. Participants were asked to make a saccade from the centrally presented stimulus toward the target dot as quickly as possible in Experiment 1, and were asked to press a button in Experiment 2. Pupil size was measured from the onset of the video until the onset of the target dot.

to perceive the different types of movements in the videos. Pupillary reactions are also slow; it was therefore necessary that the video play long enough to accurately measure pupil data. The target and the video remained on the screen until a saccade was made, or until 2000 ms had passed. Participants were instructed to move their eyes away from the target on the torso and towards the peripheral target as quickly as possible as soon as it appeared. If a saccade was made prematurely (before the onset of the target), or if the participant blinked before the onset of the target, the message ‘You moved your eyes too soon!’ appeared on the screen, and the trial was recycled to appear later in the block. If participants failed to make a saccade within 2000 ms of target onset, the trial was recycled and appeared later in the block.

The latency (saccadic reaction time) was defined as being the time between target onset and the saccade start time. At the end of a trial, a blank screen appeared for 2000 ms to allow the pupil size to return to baseline, and to give participants a short break. At the end of the experiment, participants completed a demographic questionnaire, which assessed their age and gender, the Oldfield handedness inventory (Oldfield, 1971) ($M = 69.94$, $SD = 48.19$), and the Autism Quotient questionnaire (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001) ($M = 15.84$, $SD = 6.85$) to measure autistic traits. A recent meta-analysis (Ruzich et al., 2015) found that the mean AQ score within the typical population is 16.94 (CI: 11.6–20), thus the mean AQ score of our sample of participants corresponds with the values found in the typical population.

2.1.5. Latency data analysis

Due to the experimental procedure set up (i.e. trials being recycled when participants moved their eyes too soon, blinked, or did not respond within 2000 ms), trials were not discarded due to participant errors. However, saccadic latencies less than 80 ms were discarded from the analyses (following procedures reported by Azarian et al., 2016), as they were unlikely to be triggered by the target onset; this led to a total of 3.76% of the saccade trials being removed.

Our primary aim was to investigate the effects of Motion, Agent, Autistic Traits, and their interactions, on participants’ attention. Thus, the remaining data were analysed using linear mixed-effects models with the lme4 package (version 1.1–13; Bates, Maechler, Bolker, & Walker, 2015) in R (Version 3.3.3, R Core Team, 2016). We fitted our data to maximal models, including both random intercepts and slopes insofar as possible with respect to model convergence (Barr, Levy, Scheepers, & Tily, 2013). The final, best-fitting model predicted the

time taken for participants to disengage their attention from the video and attend to the target in the periphery by modelling the interaction between Autistic Traits, Agent (a factor with 2 levels: Human or Control Agent) and Motion (a factor with 2 levels: Natural Motion or Machine-Like Motion), and including SOA (a factor with 2 levels: 2500 ms or 3000 ms) and Target Position (a factor with 2 levels: Left or Right) as covariates. All predictors were mean-centered, and the log of saccadic response time (RT) was used as the outcome variable (to correct the positive skew in the RT distribution, Baayen & Milin, 2010). A random by-participant intercept, and random slopes for Agent, Motion, and Target Position (Barr et al., 2013) were included. The R formula for our model was:

$$\text{Log(Latency)} \sim \text{Autistic Traits} * \text{Motion} * \text{Agent} + \text{SOA} + \text{Target Position} + (1 + \text{Motion} * \text{Agent} * \text{Target Position} | \text{Participant})$$

After running this model, the ‘romr.fnc’ function within the R package ‘LMERConvenienceFunctions’ (Tremblay & Ransijn, 2015) was used to exclude outliers from the model with standardized residuals greater than 2.5 standard deviations from 0. This removed an additional 3.06% of data from the analyses. Both models were compared using the ‘relLik’ function in R, which calculates the relative log-likelihood between two models, revealing that the model excluding outliers was a better fit. This method of removing outliers post-model fitting leads to fewer data points being removed, and to better-fitting models, compared to the more ‘aggressive’ removal of outliers prior to model fitting (Baayen & Milin, 2010). Plotting and inspecting the residuals for this model revealed no violations of linearity, homoscedasticity, or normality, and the correlations between the intercept and random effects were all below 0.43.

Both t and p -values are reported in Table 1 due to concerns relating to p -values estimated from linear mixed-effects models (Bates, 2006). We used $t > 2$ as a threshold for significance in all analyses in this study, which is comparable to $p < 0.05$ (Baayen, Davidson, & Bates, 2008). The p -values reported are Satterthwaite approximated using lmerTest (Kuznetsova, Brockhoff, & Christensen, 2015).

2.1.6. Pupillometry data analysis

Pupil data were cleaned prior to data analysis. Missing pupil data (e.g. data missing from blinks, etc.) were linearly interpolated, and data were baseline corrected. To perform baseline correction, the median pupil size during the first 10 ms of each trial for each participant was

Table 1
Means and Standard Deviations for each stimulus condition in Experiments 1 and 2.

	Experiment 1		Experiment 2	
	Mean	SD	Mean	SD
Human Agent Natural Motion	296.12	7.01	377.96	8.00
Human Agent Machine Motion	289.81	5.81	367.38	7.75
Control Agent Natural Motion	292.91	8.26	376.67	11.14
Control Agent Machine Motion	290.99	10.96	370.66	11.53

subtracted from the remaining data in that trial (Mathôt, Fabius, Van Heusden, & Van der Stigchel, 2018).

The epoch of interest was from the onset of the video to 2500 ms (i.e., before the onset of the peripheral target); this epoch was the same for videos with SOAs of 3000 ms. This led to 2500 data points per trial per participant. For each stimulus category, we aggregated the pupil data across time over all trials for each participant. This led to a data set consisting of 2500 data points per condition per participant.

Data obtained from 0 to 220 ms were not used for analysis as the effects of the experimental manipulation on pupil size should develop at the earliest from 220 ms, due to the latency of the pupillary response (Ellis, 1981; Mathôt, van der Linden, Grainger, & Vitu, 2015). The remaining data (220–2500 ms) were analysed with mixed-effects models via the lme4 package in R. Following Mathôt, Grainger, and Strijkers (2017), for each 10 ms time window, we conducted a linear mixed-effects model. In this model we predicted pupil size by modeling the interaction between the fixed effects: Autistic Traits, Motion, and Agent. All predictors were mean-centered. A random by-participant intercept was included, as were random slopes for the interaction between Motion and Agent. To determine the significance of the fixed effects, we set a threshold of at least 200 contiguous milliseconds where $t > 2$. The R formula for our models was:

$$Pupil\ Size \sim Autistic\ Traits * Motion * Agent + (1 + Motion * Agent | Participant)$$

Table 2
Results from the mixed-effects models investigating factors contributing to attentional disengagement in Experiments 1 and 2.

1. Experiment 1	B	SE	t	p-value
<i>Fixed Parts</i>				
Autistic Traits	0.006	0.016	0.392	0.696
Agent	0.001	0.016	0.276	0.783
Motion	0.008	0.002	3.763	< 0.001
SOA	-0.028	0.002	-15.40	< 0.001
Target Position	-0.003	0.006	-0.574	0.569
Autistic Traits * Agent	0.003	0.002	1.393	0.167
Autistic Traits * Motion	0.003	0.002	1.201	0.235
Agent * Motion	0.004	0.002	1.847	0.069
Autistic Traits * Agent * Motion	0.000	0.002	0.032	0.974
<i>Random Parts</i>				
$N_{Participants}$	49			
<i>2. Experiment 2</i>				
	B	SE	t	p-value
<i>Fixed Parts</i>				
Autistic Traits	0.036	0.019	1.906	0.062
Agent	-0.002	0.002	-1.088	0.282
Motion	0.010	0.002	5.262	< 0.001
SOA	-0.030	0.002	-16.080	< 0.001
Target Position	0.000	0.002	-0.045	0.964
Autistic Traits * Agent	0.000	0.002	-0.028	0.978
Autistic Traits * Motion	0.002	0.002	0.972	0.335
Agent * Motion	0.003	0.002	2.006	0.045
Autistic Traits * Agent * Motion	-0.001	0.002	-0.964	0.335
<i>Random Parts</i>				
$N_{Participants}$	50			

2.2. Results

2.2.1. Latency results

Results from the linear mixed-effects model (Fig. 3A and Tables 1 and 2) demonstrated that the time taken for participants to disengage from a stimulus and attend to a target was significantly influenced by the category of the stimulus presented to them. This was revealed by a significant main effect of Motion, showing that participants were slower to disengage their attention from videos of natural motion compared to machine-like motion. Furthermore, participants disengaged from the video stimulus more quickly at the 3000 ms SOA compared to the 2500 ms SOA. No other significant effects or interactions were found.

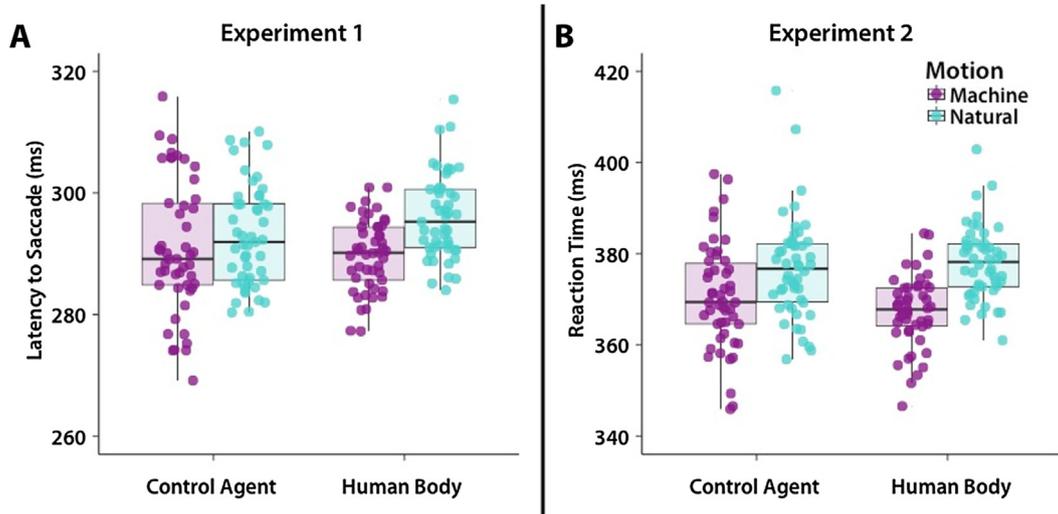


Fig. 3. (A) Experiment 1. The mean time taken (latency, in milliseconds) for participants to disengage their attention from each stimulus category to observe a target dot presented in the periphery, as measured by saccadic response times. (B) Experiment 2. The mean time taken (reaction time, in milliseconds) for participants to press a button in response to a target dot presented in the periphery. Response times are collapsed across SOA, Target Position, and Autistic Traits. The points represent individual participants, the coloured boxes represent the 25th and 75th percentiles of responses, and the whiskers represent the upper and lower values within 1.5*inter-quartile range.

Table 3

Means and Standard Deviations for significant pupil time windows for each stimulus condition in Experiments 1 and 2.

	220–480 ms		750–2200 ms		990–1570 ms			
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1. Experiment 1								
Human Agent Natural Motion	0.63	0.46	1.63	1.05	1.64	1.04		
Human Agent Machine Motion	0.62	0.45	1.58	0.92	1.60	0.92		
Control Agent Natural Motion	0.60	0.51	1.64	1.18	1.67	1.22		
Control Agent Machine Motion	0.58	0.47	1.51	1.13	1.53	1.14		
	220–510 ms		420–2500 ms		1090–2500 ms		1620–2500 ms	
2. Experiment 2								
Human Agent Natural Motion	0.23	0.21	0.67	0.55	0.79	0.58	0.82	0.62
Human Agent Machine Motion	0.23	0.20	0.66	0.54	0.79	0.57	0.82	0.61
Control Agent Natural Motion	0.22	0.20	0.72	0.53	0.85	0.54	0.87	0.56
Control Agent Machine Motion	0.20	0.21	0.61	0.51	0.73	0.53	0.74	0.56

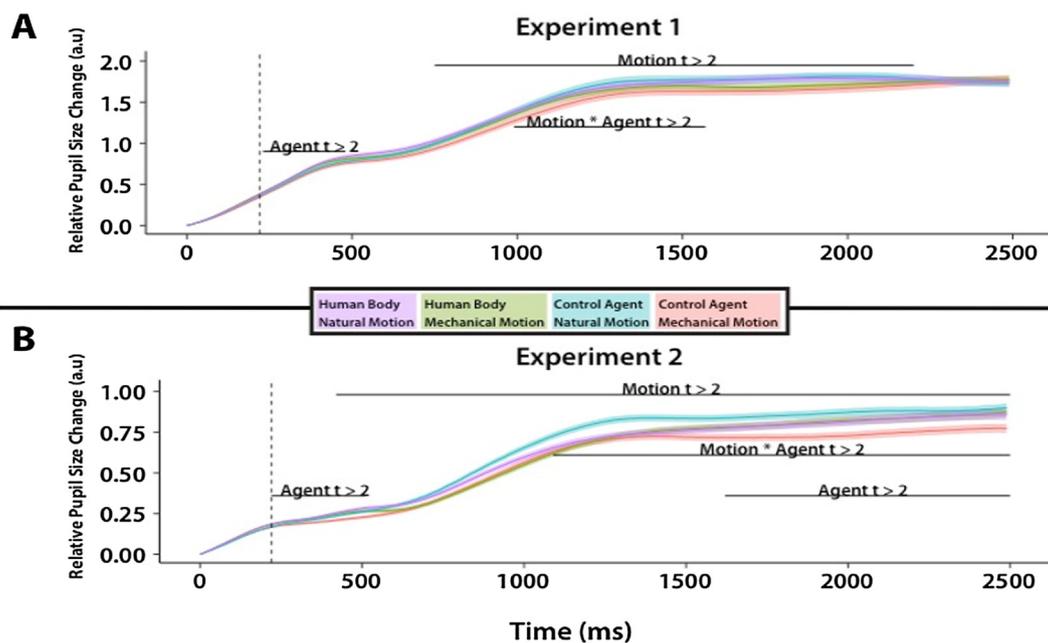


Fig. 4. (A) The change in pupil size across time, for each of the four stimulus categories in Experiment 1 and (B) in Experiment 2. In panels A and B, the shaded areas represent ± 1 SE, and the vertical dashed lines indicate that the data from 220 ms were included in the mixed-effects model. The horizontal lines indicate significant main effects or interactions ($t > 2$), as calculated by the mixed-effects models.

2.2.2. Pupil results

The results are illustrated in Table 3 and Fig. 4A. In Fig. 4A, pupil size is plotted across time. Using the significance threshold outlined above, a significant effect of Agent emerged between 230 and 480 ms, where participants showed a reliable increase in pupil size for videos of human bodies compared to control agents. Furthermore, from 750 to 2200 ms, a significant effect of Motion emerged, indicating that participants showed greater pupil dilation for videos of natural human motion compared to machine-like motion. Additionally, an interaction between Motion and Agent was present from 990 to 1570 ms, demonstrating that the difference in pupil size was larger between the two control agents than between the two human bodies. No other main effects or interactions were significant. Overall, videos of natural human motion led to greater pupil dilation among our participants, suggesting they find this kind of motion more arousing than machine-like motion.

2.3. Summary

Participants were more engaged with human body motion than with (less socially relevant) machine-like motion or motion performed by control agents. For example, participants disengaged their gaze more

slowly from natural versus mechanical motion. Their pupils also dilated earlier (220–480 ms) when viewing human versus control agents, and later (750–2220 ms) when viewing natural versus mechanical motion. We also found a significant interaction between Motion and Agent (990–1570 ms), whereby pupil size differences were greater between control agents than between human bodies. However, autistic traits did not mediate attentional engagement nor pupil dilation when viewing familiar, natural motion. Next, we examined the relationship between eye gaze, pupil dilation and biological motion by performing a conceptual replication with a new attention task.

3. Experiment 2

To replicate the attentional engagement findings of Experiment (E) 1, we used new participants and a more traditional behavioural measure (button press) of attentional disengagement (Azarian et al., 2016). We hypothesised participants would show a similar pattern of attentional disengagement behaviourally as that found in E1 with saccades, and would show increased pupil dilation when viewing videos of natural versus machine-like motion, replicating the pupillometry findings of E1.

3.1. Materials and method

3.1.1. Preregistration

Experiment (E)2 was preregistered on 4th September 2017, before any data were collected (<https://aspredicted.org/kb9p8.pdf>).

3.1.2. Participants

Fifty participants (25 females; $M_{\text{age}} = 20.34$, $SD_{\text{age}} = 2.57$) were recruited from the local community or from Bangor University's student participant panel, and were paid £7 per hour or were given course credits for their time. As in E1, we estimated the required sample size for our mixed-effects models from power calculations for repeated-measures ANOVA. This sample size of 50 participants enabled us to detect medium-to-large effect sizes with 80% power. All participants had normal or corrected-to-normal vision, provided written informed consent, and Bangor University's School of Psychology Research Ethics Committee granted ethical approval (2015-15400-A13785) following procedures in accordance with the Declaration of Helsinki.

3.1.3. Stimuli

The same four categories of stimuli were used in E2, as described in E1.

3.1.4. Apparatus

The same equipment was used as for E1. The experiment was conducted in a small, dimly lit room with no windows, and videos were presented in the center of a screen, 100 cm away from a chin rest.

3.1.5. Procedure

The task procedure was similar to that reported for E1, with the exception that participants were instructed to press the space bar as soon as a target appeared in their periphery, rather than making a saccade to the target in the periphery. If a button press was made prematurely (before the onset of the target), if the participant blinked, or if they moved their eyes before the onset of the target, the message 'You moved your eyes or responded too soon!' appeared on the screen, and the trial was recycled to appear later in the block. Failure to make a response within 2000 ms of the target onset resulted in the trial being recycled later in the block. The response time was calculated by subtracting the time of target onset from the button press time.

At the end of the experiment, participants completed the same questionnaires as in E1, including a demographic and health questionnaire, the Autism Quotient questionnaire ($M = 18.08$, $SD = 6.48$; AQ scores did not significantly differ between Experiments 1 and 2; $t(98) = -1.68$, $p = 0.096$), and the Oldfield handedness inventory ($M = 72.22$, $SD = 50.57$; scores did not differ between Experiments 1 and 2; $t(98) = -0.23$, $p = 0.819$). Note that on our Preregistration, we also stated that we planned to collect participant responses to the Social Responsiveness Scale (Constantino & Gruber, 2007). However, this questionnaire was omitted due to lack of time in the testing session.

3.1.6. Reaction time data analysis

The same reaction time data analysis procedure was followed in E2 as that outlined in E1 for the latency data. Behavioural response times faster than 80 ms were discarded from the analyses, which led to 0.07% of the data being removed. The data were modelled using linear mixed-effects models in R. All predictors in the mixed-effects model were mean-centered. Outliers were removed from the model using the 'romr.fnc' function in R, which removed an additional 2.4% of data. No violations of linearity, homoscedasticity, or normality were detected, and the correlations between the intercept and random effects were all below 0.44. The final, best-fitting model was:

$$\text{Log(Latency)} \sim \text{Autistic Traits} * \text{Motion} * \text{Agent} + \text{SOA} + \text{Target Position} + (1 + \text{Motion} + \text{Agent} + \text{SOA} * \text{Position} | \text{Participant})$$

3.1.7. Pupillometry data analysis

The same pupil data analysis procedure was followed in E2 as in E1.

3.2. Results

3.2.1. Reaction time results

The results from the mixed-effects model (Fig. 3B; Table 1) revealed that, similar to the results from E1, participants took longer to disengage their attention from natural motion compared to machine-like motion, as demonstrated by a main effect of Motion. Again, we found that participants were faster to disengage from the centrally presented stimulus at the 3000 ms SOA compared to the 2500 ms SOA. There was also a significant interaction between Motion and Agent, demonstrating that the difference in RT between motion categories was larger for the human agents than the control agents. No other significant main effects or interactions were found.

3.2.2. Pupil results

As in E1, the type of agent reliably predicted pupil size in E2 (Fig. 4B and D). In other words, participants showed a greater increase in pupil size when viewing videos of human bodies compared to control agents from 220 to 510 ms, and also to control agents from 1620 to 2500 ms. From 420 to 2500 ms, participants showed a greater increase in pupil size to videos of natural compared to machine-like motion. However, this appears to be driven by the control agent moving naturally, demonstrated by a significant interaction between Motion and Agent from 1090 to 2500 ms. This interaction demonstrated that the difference in pupil size was larger between the two control agents than between the human agents.

3.3. Summary

Participants took longer to disengage from videos of natural versus machine-like motion in the attentional disengagement task, and demonstrated greater pupil dilation for human than for control agents between 220 and 510 ms, and for natural versus machine motion from 420 ms. This effect for natural motion emerged much earlier in E2 than in E1; this was unexpected and could be due to the slight differences in experimental set-up between both experiments. We replicated the significant interaction between Motion and Agent, whereby greater differences in pupil size emerged between the control agents than human bodies. As before, autistic traits did not mediate attentional engagement and arousal when participants viewed naturalistic motion.

4. Discussion

Across two experiments, participants detected peripherally presented targets more slowly when watching an agent moving in a biologically plausible way, indicating that this stimulus type leads to greater attentional engagement. This concurs with previously published reports that attention is drawn by biological motion (Fox & McDaniel, 1982) and by other social stimuli, such as faces displaying direct gaze (Senju & Hasegawa, 2005). These results suggest that biological motion quickly and reflexively captures our attention and sustains it. To our knowledge, this is the first study to demonstrate that visual attention is more engaged by naturalistic body motion compared to other, less socially relevant motion.

We also found a main effect of SOA in both experiments. Participants disengaged attention more slowly from the central stimulus at the 2500 ms compared to the 3000 ms SOA, in accordance with previous literature (Azarian et al., 2016; Senju & Hasegawa, 2005). Future work could test the possibility that participants are still fully engaged with the videos at shorter SOAs, but begin to disengage at longer SOAs, leading to faster disengagement. Additionally, a previous study by Hedger, Haffey, McSorley, and Chakrabarti (2018) found that responses to social stimuli evolve over time, in similar timescales as

shown here. Thus, the SOA effect found in our study could be explained by the time course of social attention presented by Hedger et al. (2018).

In Experiment 2, we found a significant interaction between Motion and Figure demonstrating that the difference in RT between the two motion types was greater between the human bodies than the control agents. One possible explanation for this is that participants were more easily able to perceive the motion differences when performed by human bodies as compared to control agents.

As hypothesised, across both experiments, increases in pupil size were greater in response to naturalistic than to mechanistic motion. Sepeta et al. (2012) reported that participants have greater pupil dilation when viewing images of happy faces showing direct compared to averted gaze. Our findings are the first to show that it is not only social stimuli that signal imminent social engagement, such as faces with direct gaze, that induce autonomic changes in participants. We show that other social stimuli, such as bodies moving in a naturalistic, human-like way, induce similar autonomic changes in observers. Studies have shown that pupillary responses may be linked to reward processing (O'Doherty et al., 2006; Bijleveld et al., 2009), thus it is possible that the pupil responses observed in our study are related to the reward value of natural motion. Recently, Williams and Cross (2018) demonstrated that participants were willing to exert more effort to view videos of naturalistic human compared to mechanical motion, further reinforcing the reward value of this type of stimulus. The present findings corroborate this previous work and contribute significant new insights to our understanding of social motivation in the typical population, supporting the notion that the human body moving in a familiar way is a rewarding stimulus. However, studies have shown pupil dilation in response to arousing stimuli with either positive or negative valence (Bradley et al., 2008), thus we cannot rule out that the pupil responses observed in our study might have been due to negative responses to our stimuli. Addressing this issue of pupil dilation and stimulus valence remains an important challenge for future research to disentangle.

In both experiments, we demonstrated a significant interaction between motion and agent, whereby participants showed greater pupil dilation when viewing natural versus machine-like motion. However, later in the time course, this pupil size difference became greater between the control agents than the human bodies. In Experiment 2, the main effect of Motion appears to be driven by this interaction between Motion and Agent. The reasons for this unexpected interaction remain unclear. These findings also contrast with our latency and RT data, which demonstrate that the difference in RT between the two motion types is greater between the human bodies than the control agents. However, this unexpected pupil size finding might be partly due to the novelty of the control agent moving biologically. Our attention is reflexively captured by living beings that move similarly to us (Simion, Regolin, & Bulf, 2008); thus, the novelty of a non-human agent moving in human ways could be particularly arousing. For example, the uncanny valley hypothesis (Mori, 1970) suggests that very human-like, non-human agents are perceived as eerie, and even more so when they are moving. Therefore, the naturalistically-moving control agents used here might have increased participants' arousal due to their perceived eeriness, or violated participants' predictions of how a non-human control agent should move (c.f., Cross et al., 2012; Saygin, Chaminade, Ishiguro, Driver, & Frith, 2011). Further research is required to test this explanation, and to explain why the human body moving in a mechanical way (the other mismatch between form and motion) did not capture attention to the same degree. It is also worth noting that in both experiments, we find the smallest pupil size increase when participants view control agents moving mechanically. It is possible that the autonomic nervous system is disproportionately quiet when viewing a combination of stimulus features that are of least interest to humans.

Based on previous findings, we predicted that individuals reporting more autistic traits would engage less with natural motion. However, we found no evidence to support this hypothesis, either in the latency/RT analyses or in the pupil analysis. The range of AQ scores reported by

our two participant samples in Experiments 1 (range: 3–28, median = 15) and 2 (range: 8–33, median = 17.5) was limited, with most participants scoring towards the lower end of the distribution. While differences in attentional engagement with social stimuli may emerge at the more extreme ends of the AQ distribution, other studies have also failed to identify a relationship between social attention and autistic traits (Freeth, Foulsham, & Kingstone, 2013). Thus, it remains unclear whether reported autistic traits, or indeed an ASC diagnosis, affects attentional engagement with, and arousal from, socially relevant motion cues. Future studies should recruit both TD participants and those with a clinical ASC diagnosis to further explore this relationship.

5. Conclusions

Using an attentional disengagement task, we have shown that attention is engaged by naturalistic motion regardless of agent type. By measuring changes in pupil size, we have further shown that natural motion can lead to autonomic changes in participants. Taken together, these results complement and extend the existing social motivation literature. Not only is this the first study to demonstrate that human body motion engages participants' attention more than machine-like motion, but is also the first to associate this with changes in autonomic arousal, further supporting the notion that we value biological motion as a rewarding stimulus. Increased engagement with, and arousal in response to, viewing natural motion could relate to our innate preference to orient out attention to social stimuli, such as biological motion, that hold potentially beneficial or rewarding information. Our findings were less conclusive concerning the hypothesised relationship between autistic traits and reduced social motivation, as demonstrated by our eye-tracking measures. Further research involving both TD and participants with ASC will help to elucidate the social reward value of biological motion among individuals across the spectrum of social abilities.

Supplementary material

De-identified datasets relating to this study can be found at <https://osf.io/pdcnr/>.

Author contributions

E. H. Williams & E. S. Cross developed the study concept. All authors contributed to the study design. Testing and data collection were performed by E. H. Williams. E. H. Williams performed the data analysis and interpretation with feedback from F. Cristino and E. S. Cross. E. H. Williams drafted the manuscript and F. Cristino and E. S. Cross provided critical revisions. All authors approved the final version of the manuscript for submission.

Acknowledgements

This work was supported by funding to E.S.C. from the following bodies: a PhD studentship for E.H.W. from Coleg Cymraeg Cenedlaethol, a Future Research Leaders award jointly funded by the Economic and Social Research Council and Medical Research Council (ES/K001892/1); a Marie Curie Career Integration award (CIG11-2012-322256); and a European Research Council starting grant (ERC-2015-STG-677270). The authors would like to thank Josh Payne for assistance with data analyses.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cognition.2019.104029>.

References

- Alegria, J., & Noiroi, E. (1978). Neonate orientation behaviour towards human voice. *International Journal of Behavioral Development*, 1(4), 291–312.
- Azarian, B., Esser, E. G., & Peterson, M. S. (2016). Evidence from the eyes: Threatening postures hold attention. *Psychonomic Bulletin & Review*, 23(3), 764–770.
- Baayen, R. H., Davidson, D. J., & Bates, D. M. (2008). Mixed-effects modeling with crossed random effects for subjects and items. *Journal of memory and language*, 59(4), 390–412. <https://doi.org/10.1016/j.jml.2007.12.005>.
- Baayen, R. H., & Milin, P. (2010). Analyzing reaction times. *International Journal of Psychological Research*, 3(2), 12–28.
- Bardi, L., Regolin, L., & Simion, F. (2011). Biological motion preference in humans at birth: Role of dynamic and configural properties. *Developmental science*, 14(2), 353–359. <https://doi.org/10.1111/j.1467-7687.2010.00985.x>.
- 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.
- Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*, 68(3), 255–278. <https://doi.org/10.1016/j.jml.2012.11.001>.
- Bates, D. (2006). Lmer, p-values, and all that. Retrieved from <https://stat.ethz.ch/pipermail/r-help/2006-May/094765.html>.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.
- Beatty, J. (1982). Task-evoked pupillary responses, processing load, and the structure of processing resources. *Psychological bulletin*, 91(2), 276.
- Belopolsky, A. V., Devue, C., & Theeuwes, J. (2011). Angry faces hold the eyes. *Visual Cognition*, 19, 27–36. <https://doi.org/10.1080/13506285.2010.536186>.
- 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.
- Bradley, M. M., Miccoli, L., Escrig, M. A., & Lang, P. J. (2008). The pupil as a measure of emotional arousal and autonomic activation. *Psychophysiology*, 45(4), 602–607.
- 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.
- 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* 0803240039–0803240039.
- Chevallier, C., Kohls, G., Troiani, V., Brodtkin, 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>.
- Constantino, J. N., & Gruber, C. P. (2007). Social responsiveness scale (SRS). *Social responsiveness scale (SRS)*. 2005, 25.
- Cross, E. S., Liepelt, R., de C Hamilton, A. F., Parkinson, J., Ramsey, R., Stadler, W., & Prinz, W. (2012). Robotic movement preferentially engages the action observation network. *Human Brain Mapping*, 33(9), 2238–2254. <https://doi.org/10.1002/hbm.21361>.
- Dawson, G., Meltzoff, A. N., Osterling, J., Rinaldi, J., & Brown, E. (1998). Children with autism fail to orient to naturally occurring social stimuli. *Journal of Autism and Developmental Disorders*, 28(6), 479–485.
- 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>.
- Ellis, C. J. (1981). The pupillary light reflex in normal subjects. *British Journal of Ophthalmology*, 65(11), 754–759.
- 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, 175–191.
- 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, 1149–1160.
- Fletcher-Watson, S., Findlay, J. M., Leekam, S. R., & Benson, V. (2008). Rapid detection of person information in a naturalistic scene. *Perception*, 37, 571–583. <https://doi.org/10.1068/p5705>.
- Fox, R., & McDaniel, C. (1982). The perception of biological motion by human infants. *Science*, 218(4571), 486–487.
- Freeth, M., Foulsham, T., & Kingstone, A. (2013). What affects social attention? Social presence, eye contact and autistic traits. *PLoS One*, 8(1), e53286. <https://doi.org/10.1371/journal.pone.0053286>.
- Goldwater, B. C. (1972). Psychological significance of pupillary movements. *Psychological Bulletin*, 77(5), 340.
- Haffey, A., Press, C., O'Connell, G., & Chakrabarti, B. (2013). Autistic traits modulate mimicry of social but not non-social rewards. *Autism Research*, 6(6), 614–620. <https://doi.org/10.1002/aur.1323>.
- Hayden, B. Y., Parikh, P. C., Deaner, R. O., & Platt, M. L. (2007). Economic principles motivating social attention in humans. *Proceedings of the Royal Society of London B: Biological Sciences*, 274(1619), 1751–1756. <https://doi.org/10.1098/rspb.2007.036>.
- Hedger, N., Haffey, A., McSorley, E., & Chakrabarti, B. (2018). Empathy modulates the temporal structure of social attention. *Proceedings of the Royal Society B*, 285(1893), 20181716.
- Hess, E. H., & Polt, J. M. (1964). Pupil size in relation to mental activity during simple problem-solving. *Science*, 143(3611), 1190–1192.
- Kahneman, D., & Beatty, J. (1966). Pupil diameter and load on memory. *Science*, 154(3756), 1583–1585.
- Hess, E. H., Seltzer, A. L., & Shlien, J. M. (1965). Pupil response of hetero- and homosexual males to pictures of men and women: A pilot study. *Journal of Abnormal Psychology*, 70(3), 165.
- Kain, M. P., Bolker, B. M., & McCoy, M. W. (2015). A practical guide and power analysis for GLMMs: Detecting among treatment variation in random effects. *PeerJ*, 3, e1226. <https://doi.org/10.7717/peerj.1226>.
- Kenny, L., Hattersley, C., Molins, B., Buckley, C., Povey, C., & Pellicano, E. (2016). Which terms should be used to describe autism? Perspectives from the UK autism community. *Autism*, 20(4), 442–462.
- Kikuchi, Y., Senju, A., Hasegawa, T., Tojo, Y., & Osanai, H. (2013). The effect of spatial frequency and face inversion on facial expression processing in children with autism spectrum disorder. *Japanese Psychological Research*, 55(2), 118–130. <https://doi.org/10.1111/jpr.12000>.
- Klin, A., Lin, D. J., Gorrindo, P., Ramsay, G., & Jones, W. (2009). Two-year-olds with autism orient to non-social contingencies rather than biological motion. *Nature*, 459(7244), 257–261. <https://doi.org/10.1038/nature07868>.
- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2015). Package 'lmerTest'. *R Package Version*, 2.
- Lavie, N., Ro, T., & Russell, C. (2003). The role of perceptual load in processing distractor faces. *Psychological Science*, 14(5), 510–515.
- Mathôt, S. (2018). Pupillometry: Psychology, Physiology, and Function. *Journal of Cognition*, 1(1), <https://doi.org/10.5334/joc.18>.
- Mathôt, S., Fabius, J., Van Heusden, E., & Van der Stigchel, S. (2018). Safe and sensible preprocessing and baseline correction of pupil-size data. *Behavior Research Methods*, 1–13.
- Mathôt, S., van der Linden, L., Grainger, J., & Vitu, F. (2015). The pupillary light response reflects eye-movement preparation. *Journal of Experimental Psychology: Human Perception and Performance*, 41(1), 28. <https://doi.org/10.1037/a0038653>.
- Mathôt, S., Grainger, J., & Strijkers, K. (2017). Pupillary responses to words that convey a sense of brightness or darkness. *Psychological Science*, 28(8), 1116–1124. <https://doi.org/10.1177/0956797617702699>.
- Mori, M. (1970). The uncanny valley. *Energy*, 7(4), 33–35.
- Munafò, M. R., Nosek, B. A., Bishop, D. V. M., Button, K. S., Chambers, C. D., Percie Duset, N., ... Ioannidis, J. P. A. (2017). A manifesto for reproducible science. *Nature Human Behaviour*, 1(0021), <https://doi.org/10.1038/s41562-016-0021>.
- Murphy, P. R., Robertson, I. H., Balsters, J. H., & O'Connell, R. G. (2011). Pupillometry and P3 index the locus coeruleus–noradrenergic arousal function in humans. *Psychophysiology*, 48(11), 1532–1543. <https://doi.org/10.1111/j.1469-8986.2011.01226.x>.
- O'Doherty, J. P., Buchanan, T. W., Seymour, B., & Dolan, R. J. (2006). Predictive neural coding of reward preference involves dissociable responses in human ventral mid-brain and ventral striatum. *Neuron*, 49(1), 157–166.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, 9(1), 97–113.
- Purcell, D. G., & Stewart, A. L. (1988). The face-detection effect: Configuration enhances detection. *Perception & Psychophysics*, 43(4), 355–366.
- R Core Team (2016). R: A language and environment for ## statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Rieger, G., & Savin-Williams, R. C. (2012). The eyes have it: Sex and sexual orientation differences in pupil dilation patterns. *PLoS One*, 7(8), e40256.
- 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 nonclinical population sample of 6,900 typical adult males and females. *Molecular Autism*, 6(1), 2.
- Saygin, A. P., Chaminade, T., Ishiguro, H., Driver, J., & Frith, C. (2011). The thing that should not be: Predictive coding and the uncanny valley in perceiving human and humanoid robot actions. *Social Cognitive and Affective Neuroscience*, 7(4), 413–422. <https://doi.org/10.1093/scan/nsr025>.
- Senju, A., & Hasegawa, T. (2005). Direct gaze captures visuospatial attention. *Visual Cognition*, 12(1), 127–144. <https://doi.org/10.1080/13506280444000157>.
- 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), 17. <https://doi.org/10.1186/1866-1955-4-17>.
- Shore, D. M., & Heerey, E. A. (2011). The value of genuine and polite smiles. *Emotion*, 11(1), 169. <https://doi.org/10.1037/a0022601>.
- Simion, F., Regolin, L., & Bulf, H. (2008). A predisposition for biological motion in the newborn baby. *Proceedings of the National Academy of Sciences*, 105(2), 809–813. <https://doi.org/10.1073/pnas.0707021105>.
- Simmons, J. P., Nelson, L. D., & Simonsohn, U. (2011). False-positive psychology: Undisclosed flexibility in data collection and analysis allows presenting anything as significant. *Psychological Science*, 22(11), 1359–1366. <https://doi.org/10.1177/0956797611417632>.
- Simmons, Joseph P., Nelson, Leif D., & Simonsohn, Uri, A 21 Word Solution (October 14, 2012). Available at SSRN: <https://ssrn.com/abstract=2160588>.
- 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>.
- Sirois, S., & Brisson, J. (2014). Pupillometry. *Wiley Interdisciplinary Reviews. Cognitive Science*, 5(6), 679–692.
- Tremblay, A., & Ransijn, J. (2015). Package 'LMERconvenienceFunctions'.
- Unsworth, N., & Robison, M. K. (2016). Pupillary correlates of lapses of sustained attention. *Cognitive, Affective, & Behavioral Neuroscience*, 16(4), 601–615.

- Valenza, E., Simion, F., Cassia, V. M., & Umiltà, C. (1996). Face preference at birth. *Journal of experimental psychology: Human Perception and Performance*, 22(4), 892.
- Wang, Z., Faith, M., Patterson, F., Tang, K., Kerrin, K., Wileyto, E. P., ... Lerman, C. (2007). Neural substrates of abstinence-induced cigarette cravings in chronic smokers. *Journal of Neuroscience*, 27(51), 14035–14040.
- Williams, E. H., & Cross, E. S. (2018). Decreased reward value of biological motion among individuals with autistic traits. *Cognition*, 171, 1–9. <https://doi.org/10.1016/j.cognition.2017.10.017>.
- Woodhouse, J. M. (1975). The effect of pupil size on grating detection at various contrast levels. *Vision Research*, 15(6), 645–648.