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RESEARCH REPORT

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Distinct neural correlates of social and object reward seeking motivation

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Abstract

The "Choose-a-Movie-CAM" is an established task to quantify the motivation for seeking social rewards. It allows participants to directly assess both the stimulus value and the effort required to obtain it. In the present study, we aimed to identify the neural mechanisms of such cost-benefit decision-making. To this end, functional Magnetic Resonance Imaging data were collected from 24 typical adults while they completed the CAM task. We partly replicated the results from our previous behavioural studies showing that typical adults prefer social over object stimuli and low effort over higher effort stimuli but found no interaction between the two. Results from neuroimaging data suggest that there are distinct neural correlates for social and object preferences. The precuneus and medial orbitofrontal cortex, two key areas involved in social processing are engaged when participants make a social choice. Areas of the ventral and dorsal stream pathways associated with object recognition are engaged when making an object choice. These activations can be seen during the

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Abbreviations: ADHD, Attention Deficit Hyperactivity Disorder; AQ, Autism Spectrum Quotient; ASC, autism spectrum conditions; BDI, Beck Depression Inventory; CAM, Choose-a-Movie task; Cun, cuneus; dmPFC, dorsomedial prefrontal cortex; EPI, echo-planar imaging; FG, fusiform gyrus; fMRI, functional magnetic resonance imaging; FWE, familywise error rate correction; Hipcmp, hippocampus; IFG, Inferior frontal gyrus; LinG, lingual gyrus; MNI, Montreal Neurological Institute; mOFC, medial orbitofrontal cortex; MPRAGE, magnetization-prepared rapid acquisition with gradient echo; MRI, magnetic resonance imaging; OFC, orbitofrontal cortex; PCun, precuneus; pSTS, posterior superior temporal sulcus; SASKO, Social Anxiety and Social Competence Deficits Questionnaire (German); SID, Social Incentive Delay task; SMG, supramarginal gyrus; SPL, superior parietal lobule; SPM12, Statistical Parametric Mapping Version 12; STG, superior temporal gyrus; TE, echo time; TFT-LCD, thin-film-transistor liquid crystal display; Thal, thalamus; TR, repetition time; vmPFC, ventromedial prefrontal cortex; VS, ventral striatum; WST, Wortschatztest – German multiple-choice vocabulary test (verbal IQ).

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decision phase even before the rewards have been consumed, indicating a transfer the hedonic properties of social stimuli to its cues. We also found that the left insula and bilateral clusters in the inferior occipital gyrus and the inferior parietal lobule were recruited for increasing effort investment. We discuss limitations and implications of this study which reveals the distinct neural correlates for social and object rewards, using a robust behavioural measure of social motivation.

KEYWORDS

Choose-a-Movie-CAM task, cost-benefit, decision-making, effort, fMRI, reward, social motivation

1 | INTRODUCTION

Every day we make decisions regarding the level of social engagement we choose to have with others around us. For example, when riding the train with a friend, we may have to choose between whether to spend time engaging in a small-talk or doing a crossword puzzle on our own. The social motivation theory assumes that adults under usual conditions intrinsically assign high values to social stimuli in their environment and that this impacts their decision-making (Chevallier, Kohls, Troiani, Brodkin, & Schultz, 2012). Evidence for this emerges during early development, with infants looking more at faces rather than nonface images (Gliga, Elsabbagh, Andravizou, & Johnson, 2009; Goren, Sarty, & Wu, 1975). Interestingly, there has been research to suggest that social motivation may be reduced in autistic individuals (e.g. Chevallier et al., 2012; Dubey, Ropar, & Hamilton, 2015). The aim of the current study is to explore and identify the neural systems that support social and nonsocial choices in typically developing adults, to help direct future research aiming to understand how these processes may be operating differently in autism spectrum conditions (ASC).

Social motivation theory differentiates between three components of motivation: (a) social orientation, that is, the identification of social stimuli in the environment, (b) social maintenance, that is, the continuation of engagement with social stimuli for a long duration and (c) social seeking, that is, the behavioural effort made to engage with social stimuli that have been pleasurable in the past (Chevallier et al., 2012). One aspect of the social seeking component, namely the "liking" of social rewards, that is, the hedonic pleasure experienced when consuming, has been extensively investigated before (Berridge, 2004). However, the "wanting" aspect of social seeking has been much less investigated. This is the incentive salience that promotes the approach and consumption of rewards (Berridge, 2004). Approaching or choosing a specific option depends on its decision value, or, the benefits minus the costs (Hare, O'Doherty, Camerer, Schultz, & Rangel, 2008; Peters & Büchel, 2010). This is where the notion of effort, as cost, may come in.

A number of behavioural methods have been developed over the past several years to explore the "wanting" aspect of social seeking, however these vary greatly in the manner in which they measure this component of social motivation and whether they were conducted in children or adults. For example, in the Social Incentive Delay (SID) task, adult participants see a cue indicating that their reward on each trial will be a small, medium or large smile, or a small, medium or large cash prize (Spreckelmeyer et al., 2009). They must then respond fast to a go-signal to get this reward. The logic of the task is that participants will work harder and will react faster to get a more valuable reward. However, in the SID task participants' "wanting" of the social stimuli is estimated from an indirect measure of RT to a cue, there is no active decision between a social and nonsocial reward. Other researchers have used approach–avoidance paradigms, where participants decide whether to engage or not with social and nonsocial stimuli. They make behavioural effort such as difficult keypresses or pulling a joystick to increase their exposure to social/nonsocial stimuli. These studies found that variables such as attractiveness (Hayden, Parikh, Deaner, & Platt, 2007), gaze direction and facial expression of the social partner (Jones, DeBruine, Little, Conway, & Feinberg, 2006) and the internal emotional state of the individual (Over & Carpenter, 2009) can have a direct influence on the preference adults and children have for social stimuli. Another type of paradigm involves incentive go no-go tasks, which are very similar to the SID task. In these tasks, participants play a game of making or inhibiting a response (keypress) and their reaction time is recorded. Like SID, the cues at the beginning of the trial indicate the intensity (high/low) of the reward. The task requires to run for both social and nonsocial rewards in different blocks. Results from this type of task show that children, irrespective of their diagnostic status (typical, ASC and ADHD) have lower-error rates and faster reaction times for nonsocial monetary conditions compared to social ones (Demurie, Roeyers, Wiersema, & Sonuga-Barke, 2016; Kohls et al., 2011). Finally, choice-based tasks actually require participants to make explicit decisions between social and nonsocial stimuli and their preference is taken as an index of social seeking (Gilbertson, Lutfi, & Weismer, 2017; Ruta et al., 2017). While Ruta et al. (2017) did not see any significant preference for social stimuli in typical children, Gilbertson et al. (2017) reported higher preference for social sounds than for nonsocial ones. Importantly, on these tasks, the level of effort required to see the stimuli remains the same on all trials, hence it is hard to separate the effect of effort from the preference for stimuli.

Over the last few years, we have developed the Choose-A-Movie task (CAM). Unlike previous paradigms, the CAM task not only allows participants to make active choices for either social or nonsocial options, but also includes a systematic manipulation of choice-associated effort levels. This allows for the investigation of social motivation in relation to effort in a direct manner. In the CAM task, participants first see two abstract cues indicating which reward they can receive, with a different level of effort required for each reward (Dubey, Ropar, & Hamilton, 2015, 2017, 2018). They can choose which reward to receive by engaging in the effort task (pressing a key several times) and then receive the reward of seeing a social or nonsocial video. Thus, participants are encouraged to make a trade-off between their preference for social and nonsocial stimuli in the context of different levels of effort. The variability between levels of effort helps to disentangle the effect of effort from the stimuli preference. This task has been used to quantify social seeking in adults and adolescents with and without ASC (Dubey, Ropar, & Hamilton, 2015, 2017). Findings from the CAM task consistently show that typical adults prefer social stimuli to nonsocial stimuli, but these choices are modulated by the effort required to see each stimulus. This indicates that for typically developed people, social stimuli may have higher intrinsic value than nonsocial stimuli to start with, and when performing the task, participants must combine their estimates of the intrinsic value of the items with the cost of obtaining it. However, which regions of the brain might be involved in these processes is unknown.

There are several candidate brain systems that are known to be involved in social decision-making. To take our initial opening example of comparing the options of chatting with a friend or doing a crossword: This choice would be difficult unless the two options are evaluated using a common scale for comparison. It is suggested that the value of stimuli in the world is represented in a common currency of valuation and a large body of evidence suggests that the orbitofrontal cortex (OFC) is the core region for evaluating the stimulus general reward "value" irrespective of the nature of the stimuli (Grabenhorst & Rolls, 2011; Levy & Glimcher, 2012). Moreover, Izuma and colleagues suggest that the ventral striatum (VS) along with other brain regions might be activated in both social as well as nonsocial (i.e. monetary) reward processing (Izuma, Saito, & Sadato, 2008). On a similar line, Lin, Adolphs, and Rangel (2012) found overlap between social and monetary rewards in both the OFC and VS. However, there might also be distinct brain mechanisms tuned to rewards of different types. For example, Sescousse and colleagues (2010) reported activity of lateral OFC for monetary stimuli, but posterior OFC for erotic social stimuli. Ruff and Fehr (2014) discuss this controversy and contrast an "extended common currency scheme" with a "social-valuation-specific scheme". The former suggests that valuation for all stimuli can be localized in the same brain regions, whereas the latter implies that social valuation of stimuli is localized to specific brain regions that have evolved specifically to deal with them. If the latter is true, we might expect to find distinct brain regions involved in the CAM task when participants choose social stimuli compared to nonsocial ones.

The overarching aim of the current study is to determine what neural mechanisms are responsible for the decision-making process in the CAM task, in order to characterize this behavioural task with respect to current neural models of decision-making. Examining the decision-making phase of the task, we will test if there are distinct mechanisms engaged when people make a social choice compared to an object choice, and as they make increasingly effortful choices. Examining the reward phase of the task, we can test if viewing social stimuli engages reward areas of the brain more than viewing nonsocial stimuli.

2 | MATERIALS AND METHODS

2.1 | Participants

Twenty-four healthy adults with normal or corrected to normal vision and no history of any neurological or psychiatric condition participated in the study. There were 13 males and 11 females between the ages of 19 and 49 years ($M = 29.14$ $SD = \pm 8.28$). Participants were recruited through the local participant database. All participants gave an informed consent to participate in the study and completed a set of questionnaires (details given in procedure). They received an inconvenience allowance for their time. The study was conducted with the approval of the local ethics committee of the Medical Faculty of the University of Cologne, Germany.

2.2 | Task and stimuli

The behavioural CAM task used in the present study was based on the task previously introduced by Dubey et al. (2015). The task is found to be a robust measure of social reward-seeking motivation in typical and atypical adults and adolescents (Dubey, Ropar, & Hamilton, 2015, 2017). In the current study, we modified the CAM task used by Dubey et al. (2015) to optimize it for functional magnetic resonance imaging (fMRI) in the following way: (a) We matched the patterned boxes (stimuli linked with the movies) more closely to overcome any influence of colour/brightness on the neural activation; (b) We added a time limit for each trial and divided it into three phases, namely, a "decision phase" when the participant could view the options and prepare a decision, followed by an "action phase" where they could press keys to unlock the chosen box, and finally, the "movie phase" when they would watch the linked video stimulus from the chosen category. The task was presented on a 12 × 6.5-inch screen of a Samsung Ultrabook laptop for the practice trials and a suitable screen described below for fMRI set-up. The programme was run using a commercial software package (MATLAB R2017a; The MathWorks Inc.) with toolbox Cogent 2000 (Wellcome Department of Imaging Neuroscience, http://www.fil.ion.ucl.ac.uk/Cogent2000.html).

The video stimuli comprised 10 social movies showing adult actors looking towards the camera and smiling, and 10 object movies showing regular household objects slowly rotating over a turntable (details given in Dubey et al., 2015). All movies were of a 3 s duration and 320 pixels by 180 pixels dimensions in size. The CAM task measures participants' preference for watching movies from each of these two categories, referred to hereafter as "social choices" and "object choices".

At the beginning of the task, participants were informed that they would see two patterned boxes on either side of the screen and that each box was linked to one category of movies (Figure 1a). For example, the box with horizontal lines might be linked with social movies and the box with vertical lines linked with object movies (or vice-versa). The association between box pattern and stimulus category was counterbalanced between the participants. On each trial, participants were presented with the two boxes on the screen with one, two or three locks on each box. Participants were asked to choose which one of the two boxes they wanted to open in order to view the linked movies. This choice involved a trade-off between their preference for a particular movie category and the effort of opening more or less locks by making as many keypresses as the number of locks. If they were presented with a social box on the left with 3 locks and a nonsocial box on the right with 1 lock and if the participant would choose to open the box on the left side, their choice would reflect social over nonsocial, with a relative lock difference of +2 (locks on the left side – locks on the right side). The structure of a sample trial is detailed in Figure 1.

To correlate brain activations with different sub-processes in decision-making, each trial was divided into three phases. The *decision phase* started when a choice between two boxes was presented on the screen and ended with the appearance of a green crosshair (+) which signalled that participants could make their choice in the subsequent action phase. The decision phase of the trial lasted either 2, 4 or 6 s. In the *action phase,* the participants were asked to make the keypress as soon as possible after seeing the green crosshair, and they had a maximum of 4 s to start their first keypress before the trial elapsed. If there was no keypress within this time window, the trial was aborted and registered as invalid. As soon as the final lock was removed, the box pattern extended to fill the screen and the movie phase began. Thus, the duration of the action phase varied between 1 and 7 s. In the *movie phase*, the participant saw one movie (duration 3 s) from the category they chose. Note that movies were randomly presented within each category, so participants did not know in advance which person/object they would see. The entire trial ended with the end of the movie, and a white fixation cross appeared at the centre of the screen to indicate an intertrial interval which was pseudo-randomly jittered for 8, 10 or 12 s. Participants were instructed to fixate on the fixation cross between trials to ensure that participants' random gaze to the right or left side of the screen prior to the presentation of the stimulus would not bias their response.

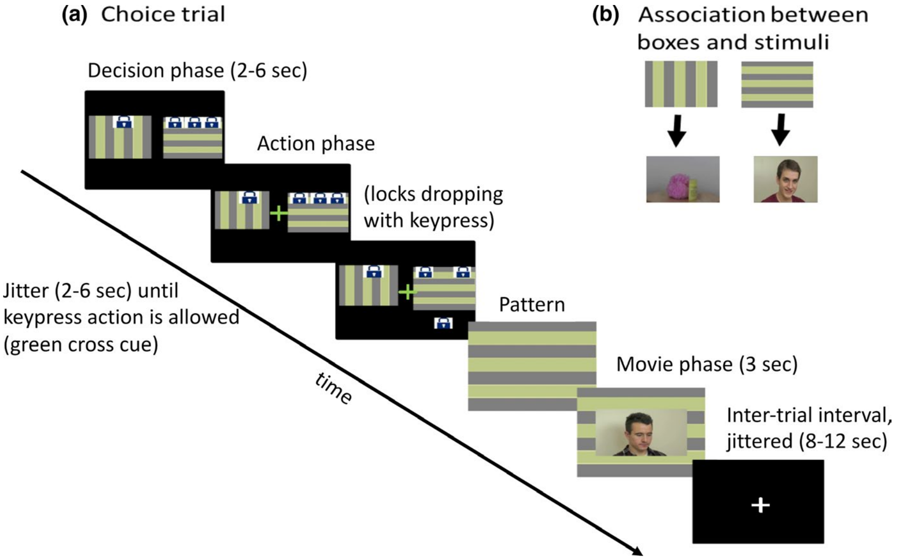

FIGURE 1 (a) Trial structure for experimental choice trials where the participant chooses the social object at higher costs. (b) Example of association between boxes and stimuli

Participants completed 120 choice trials during MRI measurements, 90 of these trials were the choice trials presenting cues for social and nonsocial stimuli with various numbers of locks (see Table S1). 30 of these trials were "effort only" trials in which participants were presented with the same patterned box, and hence the same stimulus category, on both the sides of the screen. This means that they did not have a choice between stimuli but could choose the box with the lower number of locks.

2.3 | Procedure

Participants were screened for their suitability for fMRI, and a written informed consent was obtained from them. They completed the Autism Spectrum Quotient Scale (AQ; Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001), the German versions of the Beck Depression Inventory (BDI; Beck and Steer, 1987; Hautzinger et al., 1995), the Questionnaire for Social Anxiety and Social Competence Deficits (SASKO; Kolbeck & Maß, 2009) and a German multiple-choice vocabulary test ("Wortschatztest", WST; Schmidt & Metzler, 1992).

The CAM task has previously shown a strong negative correlation between autistic traits and social seeking behaviour in nonautistic participants as well as participants with ASC (Dubey et al., 2015). Therefore, autistic traits of the participants in the current study were estimated using the AQ. All except one participant in the groups scored below the cut-off (score 35) for the general population (range = 6–39, *M* = 15.21, *SD* = ±7.17). Depression can alter the reward perception and neurophysiological activation related to reward (Alloy, Olino, & Freed, 2016; Foti, Carlson, Sauder, & Proudfit, 2014), therefore participants in the current study were evaluated for current clinical depression using BDI. The score on the BDI showed no clinical depression in any participant (range = 0–10, *M* = 1.67, *SD* = ±2.53). SASKO is a tool (in German) to measure social anxiety in typical people. It has 40 items, tapping various components of social anxiety. Social anxiety was evaluated in all the participants as it might alter the behavioural responses as well as the brain activations in response to social stimuli (Ding et al., 2011; Nakao et al., 2011). The tool could be administered on all except one participant who did not speak German. The results showed no significant deviation in social anxiety in any participant (range = 12–71, *M* = 30.55, *SD* = ±15.19). WST was used to estimate verbal IQ in the participants. It is a German multiple-choice vocabulary test (Schmidt & Metzler, 1992) known to provide a brief and valid estimate of intelligence (Lehrl, Triebig, & Fischer, 1995; Schmidt & Metzler, 1992). The participants' score (excluding one non-native German speaker participant) on WST showed average intellectual functioning (range = 27–38, *M* = 33.40, *SD* = ±2.92).

After completing all questionnaires, participants did a brief practice session of the CAM task outside the MRI environment. During this session, we ensured that participants understood the task well and learned the association between patterned boxes and stimulus categories. Immediately after completing the practice trials, participants completed the CAM task during fMRI measurement. Stimuli were presented using a custom-made, nonmagnetic high-resolution thin-film-transistor liquid crystal display (TFT-LCD) screen attached at a distance of 100 cm from the end of the scanner (viewing angle: 14 × 18 horizontal × vertical). They were displayed to participants via a mirror attached to the head coil. Participants held two MR-compatible handheld response devices (LUMItouchTM, Photon Control), one for each hand. Participants made the responses by pressing the index finger keys to choose the box on the corresponding left- or right-hand side of the screen. The task was divided into two runs of 60 trials lasting up-to 15 min each. At the end of the fMRI session participants were given an exit questionnaire to measure their attentiveness, alertness and distraction during the task on a 5 point Likert scale in which 5 meant "most" and 1 meant "least". At a group level, participants reported good attentiveness (4.21), alertness (4.04) in the first session which decreased in the second session, that is, attentiveness (3.46) and alertness (2.92). They reported medium level of distractions in first session (3.91) which remained almost the same in the second session (3.42).

3 | DATA ACQUISITION AND ANALYSIS

3.1 | Data acquisition

Functional and structural MRI were acquired on a Siemens 3T whole-body scanner with a standard head coil (PA 32) and a custom-built head holder for movement reduction (Siemens TRIO, Medical Solutions). The functional scans were taken using a T2*-weighted gradient echo-planar imaging (EPI) sequence with the following imaging parameters: TR = 2,200 ms, TE = 30 ms, field of view = 200×200 mm^2, 36 axial slices, slice thickness 3.0 mm, in-plane resolution = 3.1×3.1 mm^2. The structural scans were taken using a high-resolution T1-weighted magnetization-prepared rapid acquisition gradient echo (MPRAGE) sequence with TR = 2,250 ms; TE = 3.93 ms, field of view = 256×256 mm^2, 176 sagittal slices, slice thickness = 1.0 mm, in-plane resolution = 1.0×1.0 mm^2.

3.2 | Behavioural data analysis

The behavioural data over 90 choice trials performed by each participant was entered into a mixed model logistic regression, taking stimulus category and effort level as within-subject factors and participants' ID as between-subject factor. The model was used to predict the probability of choosing stimuli on left (p (left) $= e^t/(1 + e^t)$), where t is the difference between the utility of the boxes that is modelled as a linear function of stimuli identity on the left (x_1), relative effort on the left side (x_2) and the interaction of these two factors (x_3), hence $t = \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3$. The stimuli identity on the left could be 1 (social) or −1(object), relative effort on the left could be a number between −2 to 2 (e.g. 3 locks on left side versus 1 lock on right side would mean relative effort of −2 locks on left).

3.3 | Neuroimaging data analysis

Functional magnetic resonance imaging data were spatially preprocessed and analysed using SPM12 (The Wellcome Trust Centre for Neuroimaging) implemented in Matlab 7.1 (The MathWorks). After the functional images were corrected for head movements using realignment and unwarping, each structural image was coregistered to each participant's mean realigned functional image. All images were then normalized to the Montreal Neurological Institute (MNI) reference space using the unified segmentation function in SMP12 and were resampled to a voxel size of $2 \times 2 \times 2$ mm^3. The transformation was also applied to each participant's structural image. Functional images were then spatially smoothed with an isotopic Gaussian filter (8 mm full width at half maximum) to meet the statistical requirements of further analysis and to account for macro-anatomical inter-individual differences across participants. The normalization procedure was different for one participant, who had no anatomical data. Here, the mean functional image was computed and spatially normalized to the MNI single-subject template (Collins, Neelin, Peters, & Evans, 1994) using the unified segmentation function of SPM12 with a $2 \times 2 \times 2$ mm isotropic resolution. The ensuing deformation was then applied to the functional volumes.

The main analysis entailed a random-effects analysis (Penny & Holmes, 2004). At the single-subject level, a design matrix was fitted for each subject with regressors for each distinct phase of the trials (decision, action, movie), categorized according to the participant's choice on that trial (social or object movie). Thus, the design matrix contained regressors for (a) the decision phase for social choices, (b) the decision phase for object choices, (c) the action phase for social choices, (d) the action phase for object choices, (e) the movie phase for social choices and (f) the movie phase for object choices.

In addition, the effort made to view a chosen stimulus was defined in terms of the "lock difference" for that stimulus. For example, if a trial offered the choice between a social movie with 3 locks and an object movie with 1 lock, and the participant chose the social movie, that trial would have a lock difference of 2; that is, the participant invests the effort required to open two locks to view the social movie. If a trial offered a choice between a social movie with 1 lock and an object movie with 2 locks and the participant chose the social movie, that trial would have a lock different of −1. Thus, lock difference values range from −2 to +2 and characterize the relative effort measured in required keypresses, which a participant invests on a given trial. For all decision events, lock difference values were modelled as a linear parametric regressor, aligned with the timing of each decision phase. Note that lock difference here was calculated relative to the choice made (not the spatial location of the items), in contrast to the behavioural data analysis where we use spatial-lock-difference as a way to characterises choice behaviour.

Regressors of no interest (the "effort only" trials in which stimuli on both sides were the same and could choose the box with the lower number of locks) were also included in the design. Low-frequency signal drifts were removed using a high-pass filter with a cut-off of 128 s (Macey, Macey, Kumar, & Harper, 2004). Each event was modelled as a boxcar with the duration of that event convolved with the standard hemodynamic response function.

To localize brain regions engaged during the decision phase (the "wanting" aspect of social seeking motivation), two contrasts were calculated (decision: social > object, and decision: object > social). To localize brain regions engaged in processing the reward (the "liking" aspect of social seeking motivation, i.e. watching the chosen movies) two contrasts were performed: movie: social > object and movie: object > social were calculated. To explore the brain activation in response to effort made for social or object choices, a parametric analysis correlating the blood oxygen level-dependent response with increasing effort (−2 to 2) for both the conditions was calculated. Finally, a conjunction on the parametric effort effect for social choices and the parametric effort effect for object choices was used to localize brain regions showing a general effect of effort.

For all contrasts, SPM12 was used to compute parameter estimates (beta) and contrast images (containing weighted parameter estimates) for each contrast at each voxel. For the group-level analysis, contrast images for all participants were entered into one-sample t tests in SPM12. Brain regions that survive a cluster-level familywise error (FWE) correction of $p < .05$ (with an underlying voxel-level threshold of $p < .001$, uncorrected) over the whole brain are discussed and reported in Table 2. MRI Cro (Rorden & Brett, 2000) and the brain atlas of Duvernoy (1999) were used for anatomical localization. Activation maps were superimposed on an SPM canonical T1-weighted image.

4 | RESULTS

4.1 | Behavioural results

We found that overall choices at the group level were significantly influenced by effort (Wald $\chi^2 = 12.26$, $p = .016$) and stimuli (Wald $\chi^2 = 31.32$, $p < .0001$). This means that typical participants showed a preference for lower-effort options (i.e. a relative lock difference of −2 or −1) and a preference for social over object movies. The interaction between effort and stimuli was not significant (Wald $\chi^2 = 4.34$, $p = .361$) (see Figure 2).

4.2 | Neuroimaging results

4.2.1 | Neural correlates of decision events

We examined the neural response during decision events, when participants first viewed the patterned boxes with the locks on them and decided which category of movie they wanted to watch. On trials where participants made social compared to object choices, there was significant activation in the left cuneus and right precuneus, as well as the bilateral medial OFC (see Figure 3a; Table 1). In contrast, the neural processing during decision phases for object compared to social choices showed significantly increased neural activation bilaterally in the lingual and fusiform gyri, as well as in the right supramarginal gyrus and in a cluster that extends from the right superior parietal lobule to the right postcentral and middle occipital gyri (see Figure 3b; Table 1).

4.2.2 | Neural correlates of movie events

We examined the neural correlates of watching the chosen movies. The results show that watching social compared to object movies was linked with activation in several distinct brain areas, bilaterally, including the ventral and dorsal medial prefrontal cortex, the precuneus, clusters in the middle temporal gyri and posterior superior temporal sulci. Moreover, the right inferior frontal gyrus (pars triangularis) extending to the right precentral gyrus, the right hippocampus and the left insula were also found to be differentially activated by this contrast (see Figure 4a; Table 1). The opposite contrast of watching object compared to social movies was associated with increased neural activation in areas of the occipital lobe extending ventrally to the inferotemporal and dorsally to the parietal cortices. This included large clusters centred around the bilateral fusiform gyri and the middle occipital gyri. It also includes the right superior temporal gyrus and Heschl's gyrus, the left inferior frontal gyrus, extending to the middle frontal gyrus, the left thalamus and the left superior temporal gyrus (see Figure 4b; Table 1).

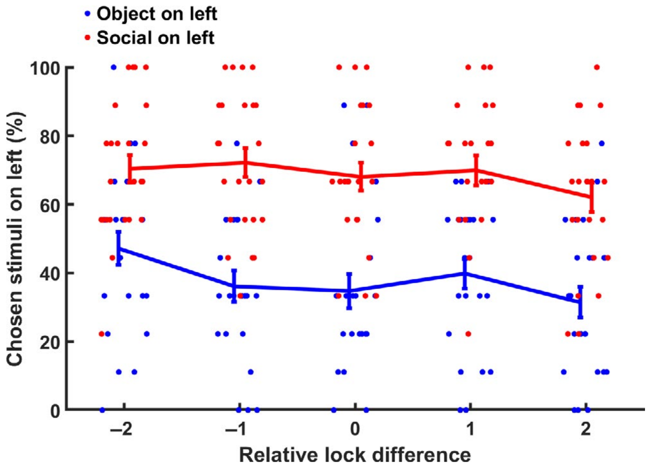

FIGURE 2 Behavioural results showing preference for social over object stimuli at all the effort levels. The difference between the lines reflects preference for one set of stimuli over other and the slope of the lines indicates the effect of effort. A −2 relative lock difference indicates that there was 1 lock on the *left side* and 3 on the *right side*. Error bars represent standard errors. Points represent individual data points

4.2.3 | Neural correlates of parametric modulation by effort

We further identified brain regions with increased neural activation when participants made social choices with more locks, that is, they involved more effort. This pattern was seen in bilateral clusters in the middle occipital gyrus extending into the inferior temporal gyrus, the left insula, the bilateral thalamus, as well as bilaterally the precentral and supramarginal gyri and the dorsomedial prefrontal cortex. Social choices with less effort were linked to increased signal bilaterally in the calcarine gyrus. We implemented the same analysis for object choices: increases in activation when participants chose an object movie with more locks were seen in the left superior temporal gyrus extending ventrally to the insula and dorsally to the postcentral gyrus, the right supramarginal gyrus, extending into the postcentral gyrus, a cluster including bilateral cerebellum activation as well as activation in the middle and inferior temporal gyri, the bilateral thalamus, the right insula, the left intraparietal sulcus, the right inferior frontal cortex and right the precentral gyrus. The opposite parametric contrast, namely looking at where the activation increased linearly with decreasing effort for decision trials where object choices were made yielded no significant activations (see Figure 5; Table 1). A direct comparison between the parametric regressors for the object movies and social movies did not reveal any distinct activations.

To identify regions which are sensitive to the amount of effort made, we implemented a conjunction of these two analyses. This identifies brain regions with an increase in signal when participants choose the option with more locks, irrespective of whether these were social or object choices. This analysis reveals bilateral clusters in the cerebellum and right inferior occipital gyrus, the inferior

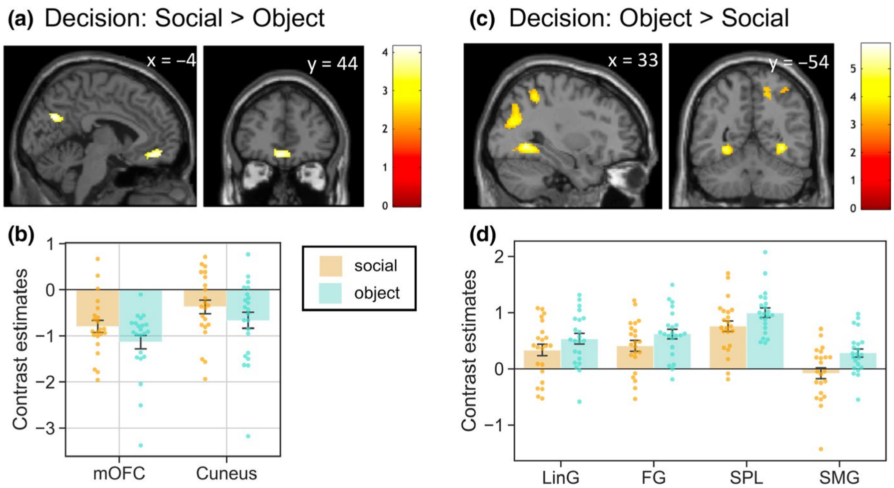

FIGURE 3 The neural response during decision events: (a) trials where participants made social choices compared to trials where they made object choices, (c) trials where participants made object choices compared to trials when they made social choices, (b, d) plots illustrate the first principle component of contrast estimates (against rest baseline) of individual voxels in the cluster of interest for the two stimulus categories. The individual points reflect contrast estimates of individual participants, and error bars reflect ±1 standard error of the mean. The principally activated voxels are overlaid on the SPM MNI T1 single-subject template image: $p < .001$, cluster-level corrected. Cun/Pcun, cuneus/precuneus; FG, fusiform gyrus; LinG, lingual gyrus; mOFC, medial orbitofrontal cortex; SMG, supramarginal gyrus; SPL, superior parietal lobule

parietal lobule, the left insula and the left postcentral gyrus (see Figure 5; Table 2).

5 | DISCUSSION

The overarching aim of this study was to identify the neural systems involved in making choices in the Choose-A-Movie (CAM) task. Choices on this task have been shown in several studies to be linked to ASC (Dubey et al., 2015, 2017) and autistic traits (Dubey, Ropar, & Hamilton, 2018), so it is useful to link this task to other models of social decision-making. Our data partly replicates the behavioural findings of Dubey et al. (2015) showing that typical adults generally prefer social over object stimuli irrespective of the levels of relative efforts between two choices. On the neural level, we found that making social over object choices is linked with activations in brain regions previously associated with social processing, that is, the medial orbital gyrus and the precuneus. Choosing object over social stimuli is linked with activations in brain areas, known to be involved in visual processing of objects, that is, the lingual and fusiform gyrus, superior parietal lobule, medial occipital gyrus and postcentral gyrus. The second aim of the study was to identify the neural correlates of an increase in relative effort to obtain social or object stimuli. Our results show that choosing the option which requires more effort was associated with increased signal in the left insula, and bilateral parietal and occipital regions. Next, we will interpret our behavioural results and then our neuroimaging findings.

5.1 | Behavioural results

In this study, we replicated the behavioural findings of Dubey et al. (2015), who found that typical adults generally prefer social over object stimuli but trade-off their preference for lower effort. However, in our previous studies (Dubey et al 2017, 2018, but not Dubey et al., 2015) using the CAM paradigm we also found a significant interaction effect of stimuli and effort on choice behaviour of typical adults and adolescents. Such an interaction would suggest a differential effect of effort on choice behaviour in extreme lock difference conditions (−2, −1, 1 and 2) compared to when both the stimuli were presented with same levels of effort (0). Interestingly, the direction of this interaction looks quite different in an adult compared to an adolescent sample (Dubey et al 2017, 2018). Moreover, the interaction effect also did not appear in Dubey et al. (2015), and we believe that the interaction reflects a floor/ ceiling effect when the strength of the preference for less effort overwhelms the social preference. Thus, the interaction itself is not a critical indicator of a trade-off in motivation, but may be an artefact of how people respond to some versions of the task. Furthermore, while lower-effort levels were preferred to higher ones, the magnitude of the effort effect appears lower in this fMRI study than in our previous behavioural studies. These differences are possibly due to the necessary adaptation made to the paradigm to optimize it for the fMRI scanner: In the behavioural version of the task, participants could start responding as soon as the trial started, and then saw the reward as soon as the button presses were finished. Here, we imposed delays in the scanner task to ensure that

TABLE 1 Cortical activations for the choice and movie events as well as parametric regressor for effort

	Cluster – level				MNI coordinates		
Region	**Size**	***p* (FWE-corr)**	**Side**	***T***	***X***	***Y***	***Z***
Decision event: Social > Object							
Cuneus	205	.033	L	4.15	−4	−68	28
Precuneus			R	3.60	6	−54	28
Medial orbital gyrus	252	.014	L	4.14	−4	44	−14
			R	3.42	4	28	−10
Decision event: Object > Social							
Lingual gyrus	363	.002	R	5.89	34	−58	−4
Fusiform gyrus	359	.003	L	5.17	−28	−52	−8
			L	4.88	−28	−62	−4
Superior parietal lobule	1,128	<.0001	R	5.00	18	−48	56
Middle occipital gyrus			R	4.63	34	−68	22
Postcentral gyrus			R	4.40	28	−46	48
Supramarginal gyrus	212	.029	R	4.23	56	−34	42
Movie event: Social > Object							
Posterior superior temporal sulcus	3,474	<.0001	R	10.53	58	−48	14
Middle temporal gyrus			R	9.71	56	−38	2
Temporal pole			R	6.43	48	16	−24
Precuneus	1,405	<.0001	R	8.19	2	−58	34
			L	6.48	−8	−54	40
Rectal gyrus	498	<.0001	R	7.35	4	42	−16
Superior medial gryus	753	<.0001	R	6.78	8	54	26
Inferior frontal gyrus (pars triangularis)	1,246	<.0001	R	6.66	42	18	28
Precentral gyrus			R	5.15	34	4	32
Superior temporal gyrus	559	<.0001	L	6.00	−58	−48	10
Hippocampus	220	.025	R	5.41	16	−8	−14
Insula	184	.049	L	4.25	−30	12	−20
Movie event: Object > Social							
Fusiform gyrus	21,425	<.0001	L	16.51	−26	−60	−10
			R	16.33	30	−50	−8
Middle occipital gyrus			L	16.27	−30	−84	12
			R	15.27	36	−84	12
Superior temporal gyrus	542	<.0001	R	5.68	64	−4	0
Heschl's gyrus			R	4.74	48	−22	10
Inferior frontal gyrus (pars triangularis)	397	.001	L	4.94	−48	34	20
Middle frontal gyrus			L	3.54	−40	42	30
Thalamus	245	.016	L	4.77	−16	−26	8
Superior temporal gyrus	262	.012	L	4.40	−56	−16	4

the haemodynamic responses were distinct for each task phase. This may have reduced the impact of the effort manipulation, because participants had to wait for the action and movie phases in all cases—that is, wait for the reward, irrespective of how many buttons they pressed. Despite this, the behaviour of participants in the scanner did replicate the overall pattern shared between all the participants performing in the previous behavioural studies. This indicates that this adapted version of the task captures the tendency to choose social over object stimuli and the effort trade-offs involved. This is depicted by participants' flexible switching to choosing object stimuli if it comes at a lower cost and not rigidly choosing either social or object stimuli. This shows the adaptations in the reward value of stimuli that people make for the item they want to see while considering the effort required to see it.

In order to ensure an optimal effort manipulation, it might be helpful to find alternate adaptations for the fMRI version of the CAM task. Such adaptations should try to ensure that an increased number of keypresses are in fact perceived as high-cost events despite the added time delay necessary to statistically isolate separate events for the fMRI analysis. This could be done perhaps by making it more difficult to unlock a higher amount of locks on the screen than a lower amount. In terms of fMRI design, researchers could waive the time delay and add a low-level control condition to capture neural processes of preparation and button presses associated with unlocking locks. This could be then subtracted from the joint decision and action phase and would represent a work-around to not having clearly separated events.

5.2 | Neural correlates of seeking of social and object movies

The primary aim of this study was to examine the brain systems involved in making rewarding social and object choices. For the "wanting" aspect of social seeking motivation, we contrasted the neural activations while participants made the decision to watch social movies or object movies. We found that when participants made social over object choices, they showed activation in medial orbital gyrus of the ventromedial prefrontal cortex and the precuneus. Making object over social choices led to activations in fusiform and parietal gyri. In both cases, these are the activations when participants make their decision, before they get to watch the social or object movies.

Previous literature suggests that the medial OFC (mOFC), a region of the ventromedial prefrontal cortex, might be a seat for value-based decision-making, especially in the cases where the value of stimuli might be altered by previous experiences and available alternatives (Rudebeck & Murray, 2014). Neurons in the OFC have been found to encode the value of offered and chosen goods (Padoa-Schioppa & Assad, 2006). The mOFC is responsible for constantly updating the value of the stimuli in relation to alternatives, hence having an important role in choice-based decision-making (Yamada, Louie, Tymula, & Glimcher, 2018). The mOFC has dense connections with the precuneus (Cavada, 2000), a posterior midline structure that was also engaged by this contrast. The precuneus has been previously involved in tasks with a valuation component. For example, it is involved in assigning subjective value to rewards (Kable & Glimcher, 2007) under risk or uncertainty (McCoy & Platt, 2005). In particular, it has been involved in the valence assessment of social stimuli (Aharon et al., 2001; Kim, Adolphs, O'Doherty, & Shimojo, 2007; Kranz & Ishai, 2006; Kringelbach, 2004; O'Doherty et al., 2003). We therefore suggest that this region is involved in assigning value to information guiding our social choices.

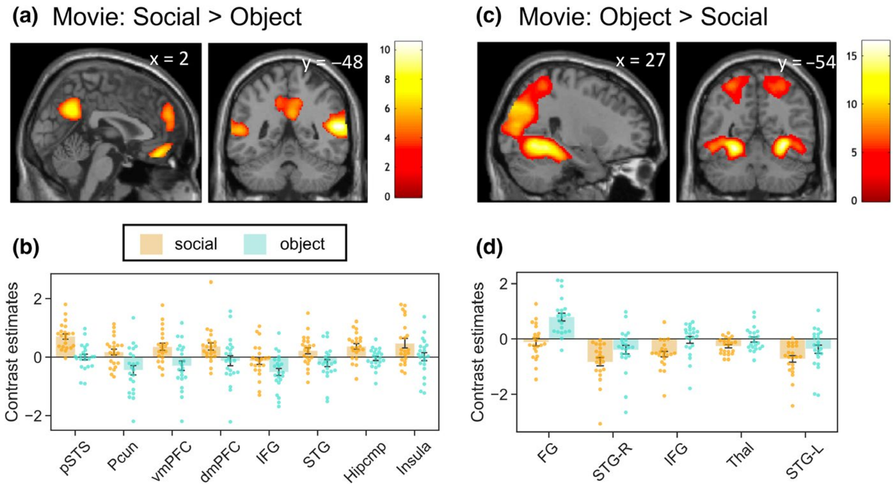

FIGURE 4 The neural response during movie events (a) trials where participants chose social stimuli, (c) trials where participants chose object stimuli, (b, d) plots illustrate the first principle component of contrast estimates (against rest baseline) of individual voxels in the cluster of interest for the two stimulus categories. The individual points reflect contrast estimates of individual participants and error bars reflect ± 1 standard error of the mean. The principally activated voxels are overlaid on the SPM MNI T1 single-subject template image: $p < .001$, cluster-level corrected. dmPFC, dorsomedial prefrontal cortex; FG, fusiform gyrus; Hipcmp, hippocampus; IFG, inferior frontal gyrus; PCun, precuneus; pSTS, posterior superior temporal sulcus; STG, superior temporal gyrus; Thal, thalamus; vmPFC, ventromedial prefrontal cortex

On the other hand, choosing the household objects rather than the social stimuli led to a significant activation in fusiform and parietal cortex. These areas are part of the ventral and dorsal stream pathways, associated with object recognition and form representation (Reddy & Kanwisher, 2006; Ungerleider & Mishkin 1982 as cited in Goodale & Mansfield, 1982). Since these activations are linked to the decision phase of the trials, it is possible that they represent an anticipation of an object. These results support the theories by Bolles, Bindra and Toates suggesting that incentive motivation emerges from a learnt stimulus–stimulus association, in which the hedonic properties of a primary stimulus are taken over by the associated cue stimulus resulting in seeking behaviour for the cue stimulus (as cited in Berridge, 2004). The studies evaluating neurobiological responses to cue and stimuli association have also suggested that dopamine neurons that are initially activated in response to the primary reward (food), shift their activation in response to the stimulus that consistently predicts food (Schultz, 1998).

For the "liking" aspect of social seeking motivation, we contrasted the neural processing while participants actually watched the chosen social or object movies. When watching social movies compared to object movies, there was increased differential activation in areas that have previously been linked to social processing and evaluation of social stimuli (Van Overwalle & Baetens, 2009): the ventromedial and dorsomedial prefrontal cortices, the precuneus, as well as the left insula and the bilateral superior temporal gyri (extending to the temporal pole in the right hemisphere). In particular, the posterior superior temporal sulci in the superior temporal gyri are specifically involved in processing the social significance of motion cues and their contribution to social communication (Gao, Scholl, & McCarthy, 2012; Zilbovicius et al., 2006). We report that a widespread activation of the social processing network is seen when observing the social movies that present human moving and smiling faces. For the opposite contrast of watching object compared to social movies, we have found differential activations in clusters of the bilateral temporal and occipital gyri that are typically associated with object recognition and the ventral visual processing stream (Goodale & Milner, 1992; Ungerleider & Mishkin, 1982 as cited in Goodale & Mansfield, 1982). In sum, the wanting and liking of social choices are associated with activations of social brain areas, whereas those involved in the wanting and liking of object choices are associated with activations of areas typically linked to object processing.

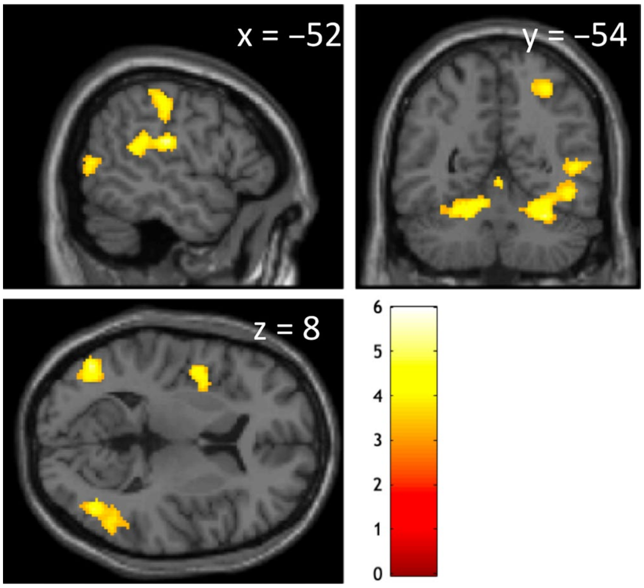

FIGURE 5 The neural response in relation to parametric effort made over trials for (a) social choices and (b) object choices

5.3 | Neural correlates of effort

To investigate the neural correlates of effort, irrespective of type of choice, we performed a conjunction analysis to look for overlapping activations for increasing effort investment. This revealed an involvement of the left insula, a region that plays a key role in processing response costs (Knutson, Rick, Wimmer, Prelec, & Loewenstein, 2007; Kuhnen & Knutson, 2005; Treadway, Bossaller, Shelton, & Zald, 2012). Moreover, we found bilateral clusters in the right inferior occipital gyrus, but also around the inferior parietal lobule extending into the postcentral gyrus. The parietal cortex activation may be related to number processing, as a region of the parietal lobe (intraparietal sulcus, see slices ± 36 in Figure 5) has been associated with mental arithmetic and quantity processing. It is also modulated by the numerical distance separating the numbers in a comparison task (Dehaene, 1996; Pinel, Dehaene, Rivière, & LeBihan, 2001). While such number processing is necessary in all conditions with a lock difference, we conjecture that in the high-effort trials, this is even more relevant as it has consequences on the subsequent behaviour (the key presses to unlock the chosen video). In addition, the conjunction analysis also highlighted the role of the cerebellum, bilaterally. The cerebellum plays an essential role in motor planning and preparation (Courchesne & Allen, 1997). We suggest therefore, that participants start to prepare their key presses as they make their choices and wait for the green crosshair event and that this is reflected even more so for the higher effort events, where the preparation of more key presses is made.

Finally, it is important to mention that previous studies on cost-benefit decision-making have mainly used probabilistic reward tasks to highlight the role of the striatum and the vmPFC, two key brain areas for reward processing, in cost-benefit decision-making. For example, in the study by Treadway, Bossaller, Shelton, et al. (2012) and Treadway, Buckholtz, et al. (2012), the authors found individual differences in dopamine function in these two brain areas. These were correlated with the willingness to invest more effort for larger rewards, a tendency that was, however, measured behaviourally in a separate session with the effort-expenditure-for-rewards-task. Similar to the CAM task, this measure also uses the number of keypresses to operationalize effort. Unlike the CAM task, however, participants were not guaranteed to get the reward if they completed the task and therefore engagement of striatum may reflect a prediction error signal (Salamone, Correa, Farrar, & Mingote, 2007; Treadway, Buckholtz, et al., 2012). Because rewards in the CAM task were not probabilistic, no activation of striatum is seen in the present task.

5.4 | Conceptual differences in social seeking across paradigms

It is useful to consider how other paradigms used to assess the neural mechanisms of social seeking conceptualize this concept by comparison to the CAM task. In the SID task, which is often used to explore neurobiological correlates of social seeking, the participants are cued about the strength of the reward they might receive at the end of the trial. For example, a circle with 3 lines would imply a high strength of social reward, which is a happy face with an open mouth smile, whereas a circle with one line would cue a low strength social reward such as a happy face with a closed mouth smile (Spreckelmeyer et al., 2009). Participants primarily respond to a reaction time task, which does not give them any control over choosing the strength or appearance/absence of the reward. Similarly, in the instrumental learning task participants learn the cues that would indicate different strengths of social reward represented by three different emotional expressions: angry, neutral and happy (Lin et al., 2012). But participants have no control over what outcome they will get, and they cannot decide about receiving or not receiving these rewards. Both these tasks quantify the neural correlates of social reward seeking as neural activation in response to reward anticipation and prediction error (failure to receive reward when it is expected), which is known to be associated with activation in the ventral striatum (e.g. Pfeiffer et al., 2014). Unlike these paradigms, in the CAM paradigm participants evaluate the value of the stimuli and then choose if they would want to look at one or the other options. Hence, they make an active decision to seeking out stimuli of their choice. Here, the strength of the reward is manipulated by presenting the stimuli with different levels of efforts. The participants choose to either make high effort to look at a preferred stimulus or choose the alternative with low effort. The valuation process here is directly influenced by both the subjective value of the stimuli ("liking") as well as the effort ("wanting"), and is known as the decision value that participants assign to the stimulus (Hare et al., 2008; Peters & Büchel, 2010). For instance, a choice for a social movie that involved high effort would suggest that the social stimulus has a high reward decision value. We believe that this kind of decision-making about investing effort or not in seeking social rewards is a conceptually closer measure of social seeking than one based on anticipation and prediction error. Taking these differences into account, it is possible that the previously used tools and the CAM task conceptualize social seeking differently, which might also result in differences in the results produced by them.

5.5 | Limitations

The results from this study are based on a small sample of 24 highly educated adults. Future research should attempt to replicate this with larger samples. Furthermore, the data collected for each condition was influenced by the choices made by the participants. For example, if participants more often chose the box with a low level of effort than that with a high level of effort, then there are fewer data points in the high effort than low-effort condition. Similarly, if participants made more often social than object choices, there are fewer data points in the object choice condition than in the social choice one. Although, in the present sample most of the participants were flexible in their choices and did not have huge variation in the data points in each condition, it is still possible that this could have imposed a major statistical limitation if we would have had participants who made choices in extreme fashion. Perhaps this limitation needs to be kept in mind when using the CAM task with atypical populations like ASC who may have a stronger preference for nonsocial stimuli (Dubey et al., 2015).

6 | CONCLUSION

This is the first study to examine the neural correlates of the decision process using a well-controlled task that allows an active choice in participants without uncertainty in the outcome of each choice. In addition, it includes a manipulation of effort required to attain a certain reward. In sum, we found that making social over object choices has distinguishable neuronal activations. These activations can be seen during the decision phase even before the stimuli have been viewed, indicating a transfer the hedonic properties of a social stimulus to its cues. This study raises important question about the conceptualisation of social seeking motivation behaviour and how the reward value of social interaction ("wanting") can be determined by their subjective value ("liking") as well as by the effect of the additional factors like effort.

TABLE 2 Cortical activations for increased level of effort for both social and object choice

Parametric decision: Increasing social effort (−2 to 2)							
Middle occipital gyrus	8,003	<0.0001	R	6.27	44	−66	4
Fusiform gyrus			R	6.15	40	−62	−14
Middle occipital gyrus			L	5.74	−44	−70	4
Middle temporal gyrus			L	5.72	−46	−68	6
Inferior occipital gyrus			R	5.66	40	−68	−8
Thalamus	1,447	<0.0001	R	5.97	22	−30	6
Pallidum			R	5.45	20	−6	−2
Thalamus			L	5.04	−12	−8	−6
Supramarginal gyrus	2,582	<0.0001	R	5.97	58	−16	22
Postcentral gyrus			R	5.51	56	−18	46
Rolandic operculum	1,821	<0.0001	L	5.95	−44	−28	18
Postcentral gyrus			L	5.59	−56	−20	18
Supramarginal gyrus			L	5.18	−44	−36	24
Rolandic operculum	295	0.007	L	5.22	−42	−4	12
Insula			L	4.12	−42	2	4
Superior medial gyrus	291	0.008	L	4.53	−8	56	26
Superior medial gyrus			R	3.58	6	58	24
Parametric decision: Decreasing social effort (2 to −2)							
Cuneus	716	<0.0001	L	4.68	0	−78	32
Calcarine gyrus			R	4.47	4	−70	12
Cuneus			R	4.13	8	−82	18
Calcarine gyrus	211	0.030	R	4.64	20	−50	6
Parametric decision: Increasing object effort (−2 to 2)							
Insula	2,794	<0.0001	L	6.99	−38	0	8
Superior temporal gyrus			L	5.80	−44	−38	22
Postcentral gyrus			L	5.77	−56	−20	20
Supramarginal gyrus	2,493	<0.0001	R	6.92	60	−16	22
Inferior parietal lobule			R	5.26	34	−46	50
Postcentral gyrus			R	5.17	60	−20	40
Cerebellum	2,324	<0.0001	R	5.94	28	−54	−24
Lingual gyrus			R	5.16	24	−88	−14
Middle temporal gyrus			R	5.07	42	−68	14
Inferior temporal gyrus			R	4.50	48	−52	−14
Thalamus	414	0.001	L	5.90	−16	−10	−2
Middle temporal gyrus	2,056	<0.0001	L	5.81	−46	−68	6
Cerebellum			L	5.23	−26	−56	−24
Insula	276	0.010	R	5.42	40	2	12
Superior frontal gyrus	501	<0.0001	L	5.36	−6	−2	68
Dorsal anterior cingulate gyrus			R	3.82	4	−4	48
Thalamus	235	0.019	R	5.21	14	−12	−6
Intraparietal sulcus	407	0.001	L	4.60	−36	-48	52
Postcentral gyrus			L	3.98	−20	−50	56
Inferior frontal cortex	205	0.033	R	4.58	58	12	16

(Continues)

TABLE 2 (Continued)

Precentral gyrus	295	0.007	R	4.30	48	0	42
Conjunction (Social + Object): Parametric decision: Increasing social effort (−2 to 2)							
Supramarginal gyrus	1,555	0.000	R	5.97	58	−16	22
Inferior parietal lobule			R	5.09	36	−46	54
Postcentral gyrus			R	4.81	60	−18	46
Middle temporal gyrus	1,534	0.000	L	5.72	−46	−68	6
Cerebellum			L	4.74	−16	−52	−22
Fusiform gyrus			L	4.59	−30	−66	−12
Postcentral gyrus	705	0.000	L	5.45	−56	−20	20
Rolandic operculum			L	5.35	−44	−32	22
Supramarginal gyrus			L	5.09	−52	−22	22
Rolandic operculum	255	0.014	L	5.16	−42	−4	12
Insula			L	4.21	−42	2	4
Cerebellum	1,739	0.000	R	5.15	30	−54	−26
Inferior occipital gyrus			R	4.91	28	−88	−12
Middle temporal gyrus			R	4.78	42	−68	10
Postcentral gyrus	189	0.023	L	4.42	−52	−22	46

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CONFLICT OF INTERESTS

The authors declare that they have no competing interests.

AUTHOR CONTRIBUTIONS

ID, DR and AH designed the paradigm; AG, ID, AH and KV adapted the paradigm for the fMRI; ID, AG and AH analysed the data; ID, AG and MH recruited participants and collected data, KV supervised data collection. ID, AG and AH wrote the paper. MH, DR and KV critically revised the manuscript. ID and AG contributed equally as first authors.

ETHICS STATEMENT

The study was conducted with approval of the local ethics committee of the Medical Faculty of the University of Cologne.

DATA AVAILABILITY STATEMENT

The datasets generated & analysed in this study are not publicly available because the participants did not consent to data sharing. Anonymised second level analyses are available from the corresponding author on request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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