Biological Motion Feedback As Rewarding Stimuli To The Brain

A novel fMRI study on biological motion

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Abstract: Human social motivation is characterized by the pursuit of social reward and the avoidance of social punishment. However, most previous studies have focused on using human faces as social stimuli and little is known about responses of the different populations to other types of social stimuli, such as biologial motion. Biological motion is defined as the visual perception and integration of movement associated with human/animal movement and provides rich information about the identity of an agent as well as the actions and intentions conveyed in the way an agent moves. The aim of the present study was to investigate whether typically developing individuals also assign a high value to positive/negative motion stimuli as feedback as they do with faces and whether the preference for this type of social stimuli is also linked to autistic traits. Thus, we conducted an event-related functional magnetic resonance imaging (fMRI) experiment using a social incentive delay task with dynamic video stimuli of body motion alone (masked faces) as social incentive feedback in order to examine participants' motivation for social reward gain and social punishment avoidance. The anticipation phase analysis revealed significant activation of the right thalamus during the avoidance of punishment condition, showing a greater activation when comparing negative biological motion feedback to negative text feedback. Moreover, we found significant activation of brain areas linked to specific processing of biological motion in all the other condition as well as in the outcome phase. Taken together, these results might provide initial evidence of biological motion feedback possibly being more rewarding to the brain than text feedback.

Keywords: thalamus, social reward, social punishment, biological motion

1. Introduction

The Social Motivation Theory is the idea that social motivation plays a central role in human development and has recently gained interest. This theory emphasizes impact of activity and actions mediated through social interaction, and within social contexts. It extends the social aspects of the Cognitive Evaluation Theory, which highlights the important role of positive feedback from others during action, but requires the individual as the internal source of causality (internal motivation). On the other hand, the Social Motivation Theory predicts that motivation has an external source of causality and is socially distributed among the social group (external motivation) (Ryan & Deci, 2000). Social motivation can be described as a set of psychological dispositions and biological mechanisms biasing the individual to preferentially orient to the social world (social orienting), to seek and take pleasure in social interactions (social seeking), and to work to foster and maintain social bonds (social maintaining) (Chevallier, Kohls, Troiani, Brodkin, & Schultz, 2012). Social orienting means that human beings prioritize information that is potentially beneficial or rewarding. An example can be observed very early in life where infants have shown to preferentially attend to face-like stimuli instead of scrambled or inverted faces (Gliga, Elsabbagh, Andravizou, Johnson, 2009; Rosa Salva, Regolin, Vallortigara, & Johnson, 2011). Faces have been shown to be very salient stimuli and highly relevant social signals that facilitate social tasks, such as gender discrimination or encoding face identities (Senju & Johnson, 2009). Seeking and liking describes the next step where we do not only orient to social cues but we find them rewarding. Behavioral economic studies have shown that adults exert effort to obtain social rewards (Hayden, Parikh, Deaner, & Platt, 2007), which highlights their incentive value, and that players in economic games report taking pleasure in mutual cooperation (Fehr & Camerer, 2007). Moreover, when given the choice to access a reward collaboratively or individually, toddlers strongly prefered collaboration (Rekers, Haun, & Tomasello, 2011). Therefore, social interactions seem to have an intrinsic motivational value. People typically engage in prosocial behaviors not because they expect direct benefit but because they find it inherently rewarding. Social psychologists have thus argued that the overjustification effect, which occurs when an expected external prize decreases a person's intrinsic motivation to perform the task (in ther words, rewards are no longer offered, intrinsic motivation does not return and prizes must be continously offered to sustain activity) (Carlson, Heth, Miller, Donahoe, & Martin, 2010), provides evidence that prosocial behavior constitutes its own reward and is intrinsically motivated. Finally, social maintaining describes the effort and desire individuals show to engage with others over long periods of time. Research has shown that this behavior emerges early in development with preschoolers spontaneously engaging in positive self-presentation (Talwar, Murphy, & Lee, 2007; Fu & Kang, 2008; Ross, Smith, Spielmacher, & Recchia, 2004). In addition, there is evidence that people unconsciously mimic others' nonverbal manners and that they do so because perceived similarity is an important predictor of likeability (Lakin, Jefferis, Cheng, & Chartrand, 2003). More empathic individuals (Chartrand & Bargh, 1999) and people scoring high in measures of social motivation (Lakin & Chartrand, 2003) have show to exhibit stronger mimicry as well.

With such defined behavioral responses, recent efforts have been made in order to study the neural mechanisms of social motivation. One of the methodological approaches designed to test the Social Motivation Theory that has been widely used by scientists is the social incentive delay task

(SID), which is an adaptation of Knutson's monetary incentive delay task (Knutson et al., 2005, 2000), and aims to examine participants' motivation to receive social rewards (Rademacher et al., 2010; Spreckelmeyer et al., 2009). Since its introduction in 2000 the monetary delay task has served to explore the neural underpinnings of reward processing in the brain. This task consists on presenting a series of stimuli, usually images of shapes, each associated with either reward (monetary gain) or punishment (monetary loss or no gain) and asking participants to react to a target stimulus after receiving the incentive cue but before the reward is given. Because the reward is only given depending on the reaction time of the participant, contingency can be introduced to make the reward less predictable. This paradigm allows investigation of different stages of reward processing, like reward anticipation, outcome processing, and consumption, as well as the processing of tasks under different reward conditions (Lutz & Widmer, 2014). Several structures have been identified and thought to play an important role, for example Knutson and colleagues (Knutson, Fong, Adams, Varner, & Hommer, 2001) reported that reward anticipation activated ventral striatal regions, whereas the receipt of reward outcomes activated the ventromedial frontal cortex, thus replicating earlier studies in monkeys (Schultz, Tremblay, & Hollerman, 2000) (Figure 1).

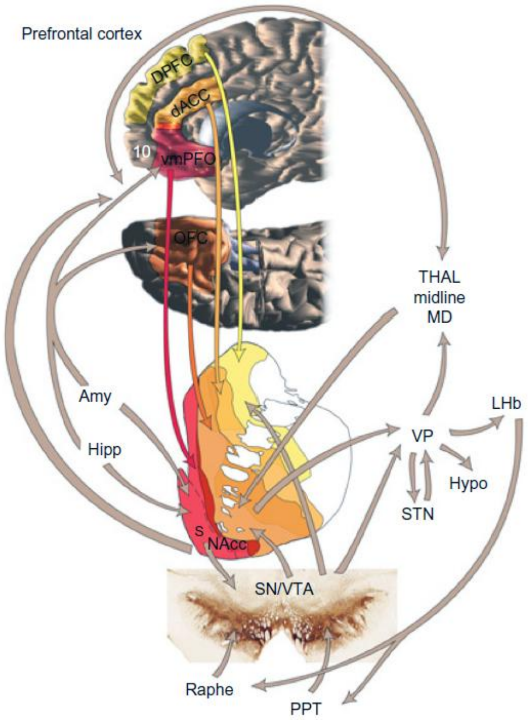


Figure 1. The human reward circuit. Evidence from various studies highlight the key role of the nucleus accumbens (NAcc) and the ventral tegmental area dopamine neurons in the human reward circuit. However striatal and midbrain areas involved during reward processing are more extensive than previously thought, including the entire ventral striatum and the dopamine neurons of the substantia nigra, respectively. Thereby, the orbital frontal cortex (OFC) (dark orange arrow) and the anterior cingulate cortex (ACC) (light orange arrow) provide the main cortical input to the ventral striatum. Moreover, the ventral striatum receives substantial dopaminergic input from the midbrain. On the other hand, ventral striatum projections target the ventral pallidum and the ventral tegmental area/substantia nigra, which, in turn, via the medial dorsal nucleus of the thalamus (Thal), project back to the prefrontal cortex. Additionally, other structures, such as the amygdala (Amy) and the hippocampus (Hipp) play a key role in the regulation of the reward circuit. ©2010 *Neuropsychopharmacology* (Haber & Knutson, 2010).

More importantly, research conducted using the SID task has suggested neural sensitivity to social rewards and punishments in several cognitive impairments as well. Kohls and colleagues published a study suggesting a reward system dysfunction in Autism Spectrum Disorders (ASD) in response to both monetary and social rewards. In particular, they reported diminished activation in the nucleus accumbens for monetary rewards as well as hypoactivation of the amygdala and anterior cingulate cortex in response to both types of reward. Thus, they suggested the reward circuitry of ASD to be compromised in social and non-social responses which was likely to contribute to atypical motivated behavior (Kohls et al., 2013). Furthermore, in 2015 research found an imbalance in the neural motivational system as an underlying mechanism of Social Anxiety Disorders (SAD). They found a valence-specific interaction with group in the left putamen and decreased putamen-ACC connectivity compared to controls on both reward and punishment trials. It was concluded that cortical control processes during social incentive anticipation and the usual motivational preference for social reward were disrupted in SAD (Cremers, Veer, Spinhoven, Rombouts, & Roelofs, 2015).

Most of the research involving the SID task has typically used static images of happy vs. angry faces as rewarding stimuli. However, Kohls and colleagues incorporated videos of actors and actresses displaying either a neutral face, a positive rewarding (e.g. a happy smiling face while performing a thumbs up) or a negative punishing behavior (e.g. a disappointed expression while performing a thumbs down) in a SID experiment performed inside the scanner in order to increase the ecological validity of the stimuli. The experiment was divided into two tasks: 'approval' or 'avoidance of disapproval' (Figure 2).

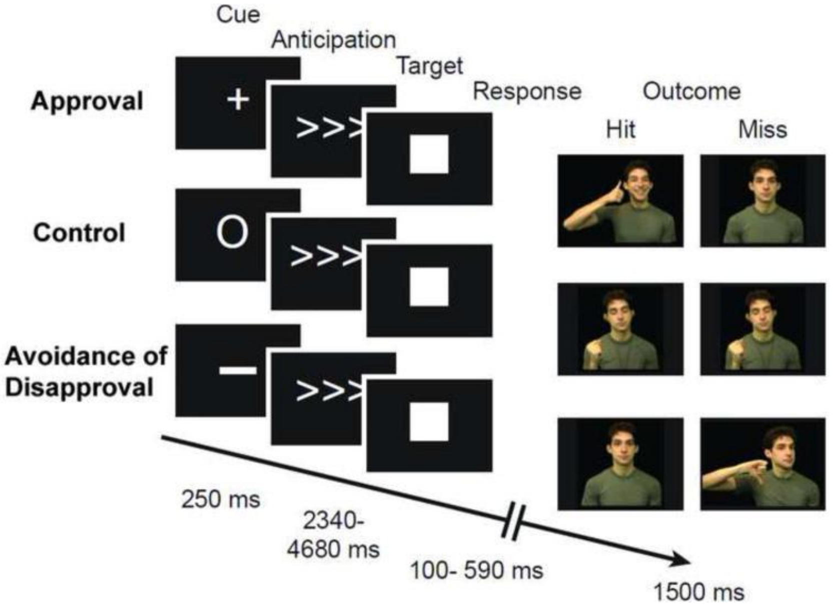


Figure 2. Illustration of the social incentive delay task including two different task versions: (1) seeking social approval (APR), and (2) avoiding social disapproval (AVOI). Each task comprised a total of 48 incentive trials and 48 control trials (in addition to null events) presented across six runs in total, three for each task type, with intermixed incentive and control trials in each run. To increase the ecological validity of the paradigm, static photos were replaced with short movie clips of actors expressing facial expressions along with other nonverbal gestures (e.g. thumbs up, thumbs down) (Kohls et al., 2013).

They reported recruitment of the ventral striatum (VS), the nucleus accumbens (Nacc) and the thalamus, in the anticipation of both avoiding disapproving stimuli, and obtaining rewarding stimuli. Stronger VS/Nacc activity was accompanied by faster reaction times of the participants to obtain those desired outcomes, corroborating prior findings in the non-social domain (monetary gain or loss) which likely reflect motivation to obtain reward and avoid punishment (Kohls et al., 2013).

Nonetheless, as these previous studies investigating social motivation have focused on using social stimuli such as human faces, little is known about responses of the different populations to other types of social stimuli, such as biologial motion. Biological motion is defined as the visual perception and integration of movement associated with human/animal movement. It provides rich information about the identity of an agent as well as the actions and intentions conveyed in the way an agent moves (Rutherford & Kuhlmeier, 2013). For example, individuals have been shown to be better at identifying themselves compared to others when looking at a point-light display (Troje & Westhoff, 2006). Participants were presented with a static or dynamic visual consisting of small, circular light sources places on the major joints that allow movement in humans. These figures are called point-light displays (Blake, 1993). Participants were able to recognize different emotions as well as perform gender identification from the point light-displays by attending to body language.

In a recent behavioral experiment, conducted by Williams and Cross (manuscript under review), the social value of biological and non-biological motion was investigated in a typically developing (TD) adult population whose self-reported autistic traits were also measured. In this study, a modified version of the Choose-A-Movie (CAM) paradigm was used (Dubey et al., 2015) which provides an index of the effort participants are willing to exert in order to watch different videos (e.g. human biological motion, machine non-biological motion). Participants were asked to choose to open one of two boxes based on their prior knowledge of the content of said boxes (e.g. green box was always associated with human motion) and the number of locks each box contained (3 locks required more key presses, and thus more effort to open, than a box with only 1 lock). Their results suggest that autistic traits significantly predicted the type of stimulus participants chose to watch. The population with more autistic traits preferred to watch videos that were the least social and participants with fewer autistic traits preferred to watch the videos that were more social. Based on these results, it was suggested that participants with more autistic traits value these type of social movement stimuli less than those with fewer autistic traits (Williams & Cross, under review).

Due to the results found with moving stimuli where typically developing populations have assigned value to moving faces as feedback and the connection to how this process might be modulated by autistic traits we decided to follow Kohls and colleagues' steps for our study, interested in the reward assignation of biological motion as a form rewarding or punishing feedback in the population. In addition, based on the results of the aforementioned behavioral experiment where a correlation between autistic traits and preference of social reward was observed, we ought to fill the gap on the research looking into the neural responses to biological motion as rewarding/punishing feedback. As a result, our study focused on social seeking interactions. The aim of the present study was to investigate whether typically developing individuals also assign a high value to positive/negative motion stimuli as feedback as they do with faces and whether the preference for this type of social stimuli is also linked to autistic traits. In order to do so we used a modified version of the Social Incentive Delay task (SID), originally developed by Knutson and colleagues (2000, 2005), that allow us to examine the participants' motivation to receive social rewards. In our modified version an extra condition was added, a text condition was incorporated in the form of feedback (text feedback) for all types of stimuli (positive, negative, and neutral) in order to find whether elicited brain activation was more robust for body motion-feedback processing or if, on the contrary, they resulted from a wider conceptualisation of feedback per se.

We hypothesised that 1) approving (reward) and disapproving (punishment) body motion would activate similar brain regions that have been found activated for monetary and facial rewads (i.e. ventral and dorsal striatum, nucleus accumbes, thalamus, and orbitofrontal cortex) compared to the text conditions (APR/AVOI MOTION > TEXT) and 2) approving and disapproving body motion would elicit higher activation compared to controls (APR/AVOI > CONTROL) in reward-related brain regions.

2. Methods

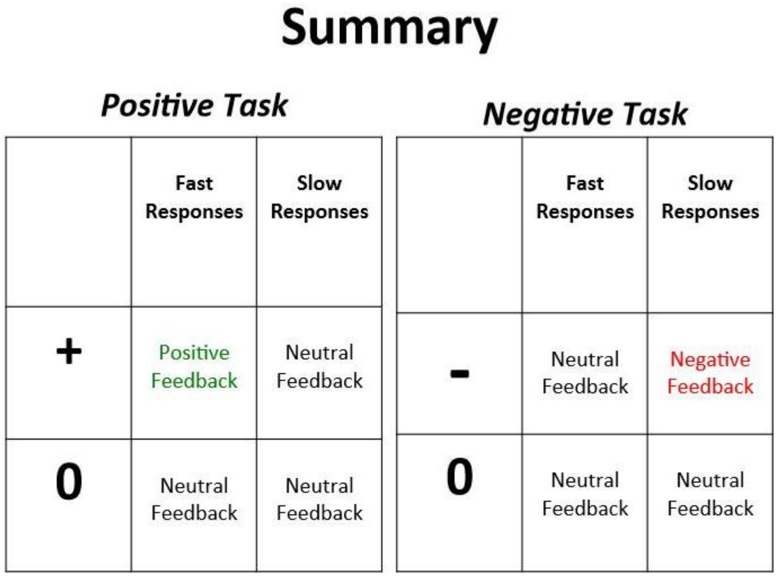
2.1. *Subjects*

Study participants were recruited from Bangor University graduate and undergraduate student community through the internal SONA system, posters, word-of-mouth and social media. The initial sample consisted of 32 right-handed healthy volunteers with normal or corrected-to-normal vision. Data from 9 participants were incomplete and could not be used for data analyses (e.g. missing logfiles). Subsequently, 1 participant was excluded due to excessive head movements during the fMRI scan (i.e. more than 1.5mm of translational motion in the *x*, *y*, and *z* direction throughout the course of a run). Thus, the final sample comprised 22 volunteers (15 females, 7 males; mean age: 23.4, SE_m: 0.7; range: 19-34 years). All denied a history of psychiatric and neurological problems. None reported taking medications affecting the central nervous system at time of testing or within the last two months. All participants gave written informed consent to be part of this study, which was approved by the local Research Ethics Committee of the School of Psychology at Bangor University (Ethical Approval Code: 2017-15913). Volunteers were compensated for their participation with either course credits or £20.

2.2. *Research design*

Before the scanning participants completed a pre-screening session where, after providing written informed consent, they completed a demographic questionnaire assessing their age, gender and education, an Adult Autism Spectrum Quotient (AQ) questionnaire (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001), and lastly the Edinburgh Handedness Inventory (EHI) (Oldfield, 1971). In addition, participants were trained in the task they were to perform in the fMRI scanner (Figure 3) for them to familiarise with the task as well as obtaining their individual average reaction times (RTs).

For the fMRI session a Social Incentive Delay task (SID) was used (Kohls et al., 2013); this task is an adaptation of Knutson's monetary incentive delay task (Knutson et al., 2005, 2000), and aims to examine participants' motivation to receive social rewards (Rademacher et al., 2010; Spreckelmeyer et al., 2009). Due to the nature of our study and hypothesis a modified version of the SID task was used. On each trial of the SID task, participants in the scanner had to perform a reaction task where they were instructed to press a button as soon as they saw a white square appear on the screen. The task was divided in four runs, each run consisted of 4 mini-blocks which could be either positive or negative. In the positive blocks two types of feedback could be presented: positive or neutral feedback in the form of videos or text. Positive videos depicted approving body motion (e.g. thumbs up, clapping) while neutral videos showed neutral body motion (e.g. rocking back and forth, adjusting t-shirt). In addition there could be positive static text ("good job", "fantastic") or neutral text ("next trial", "get ready"). In negative blocks two types of feedback could be presented: negative or neutral feedback in the form of videos or text. Negative videos depicted punishing body motion (e.g. thumbs down, angry sideways movement with the fist) while neutral videos showed neutral body motion (e.g. rocking back and forth, adjusting t-shirt). In addition there could be negative static text ("not fast enough", "try again") or neutral text ("next trial", "get ready") (Figure 3). The text condition was added in order to find whether brain activation patterns were more robust as a result of body motion feedback or if, on the contrary, they were a result of a wider conceptualisation of feedback per se. Participants were informed of the type of feedback they were going to receive via an additional slide displaying the name of the block (e. g. video feedback or text feedback) set before the cue (Figure 4).



Summary

Positive Task

	Fast Responses	Slow Responses
+	Positive Feedback	Neutral Feedback
0	Neutral Feedback	Neutral Feedback

Negative Task

	Fast Responses	Slow Responses
-	Neutral Feedback	Negative Feedback
0	Neutral Feedback	Neutral Feedback

Figure 3. Summarized table of the two tasks presented to participants in the screening session. In positive tasks two cues could be shown, **+** or **0**, indicating the type of feedback they would receive depending on the reaction time of their response. In + trials feedback was positive when reaction times were low and neutral when they weren't. **0** indicated control trials where feedback was kept neutral regardless of the response time. In negative tasks, clues were **-** or **0** being - used to denote neutral feedback when reaction times were low and negative feedback when they were high.

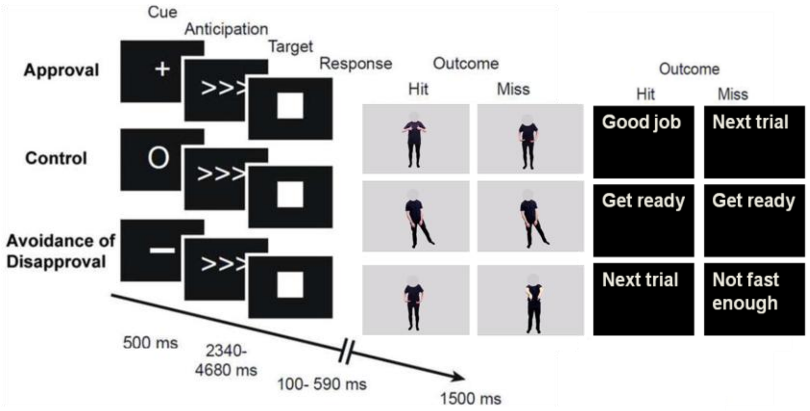


Figure 4. Illustration of the social incentive delay task including two different task versions: (1) seeking social approval (APR), and (2) avoiding social disapproval (AVOI). Each task comprised a total of 80 trials presented across four runs in total. Each run consisted of 4 mini-blocks, 2 blocks displaying motion feedback and 2 blocks displaying text feedback. There were 20 trials within each mini-block, 10 incentive trials and 10 control trials. Both, blocks and trials, were randomized in order to prevent participants from guessing which feedback videos were going to be displayed next. To increase the ecological validity of the paradigm, static photos were replaced with short movie clips of actors expressing positive, negative, or neutral body feedback gestures.

2.3. fMRI procedure

All imaging data were collected using a Philips 3T scanner (Bangor, United Kingdom) and a 32 multichannel head coil. Functional data consisted of four 12-minute runs of whole-brain T2* weighted BOLD echoplanar images with 330 volumes acquired per run (40 oblique axial slices, isotropic voxel size = 3.5 mm, TR/TE = 2340/30 ms, flip angle = 90°). One high-resolution structural MR image was acquired for the registration of fMRI data to MNI space: A T1-weighted sequence collected in the same plane as the fMRI data (number of slices = 40, slice thickness = 3.00 mm, TR/TE = 18/3.5 ms, flip angle = 8°).

2.4. *Data analysis*

Image processing and statistical analyses were carried out using FSL (v4.1.6). For pre-processing, functional volumes for each participant were skull-stripped, motion-corrected, temporally high-pass filtered, and spatially smoothed using a Gaussian kernel (FWHM=5mm). Functional data were registered to MNI space using affine transformations using FLIRT.

The first-level model for the within-run analyses of each task included regressors following a two (incentive: [APR vs. CON] or [AVOI vs. CON]) by condition (task: motion/text) by two (HIT vs. MISS) design: ANT APR Hit, ANT APR Miss, ANT AVOI Hit, ANT AVOI Miss, ANT CON Hit, ANT CON Miss. Following Kohls et al., 2013, hit and miss trials were modelled separately, since animal research has shown that VS/Nacc signals to reward-predicting cues are significantly greater when subsequent operant responses to the cues are accurate (i.e. hit) rather than inaccurate (i.e. miss) (Francois, Conway, Lowry, Tricklebank, & Gilmour, 2012; Nicola, Yun, Wakabayashi, & Fields, 2004). The anticipation phase model included the duration of the variable interval between cue onset and feedback onset (~1-2 TR jittered). Control trials served as a baseline. Furthermore, in order to discard the idea of an Nacc involvement in a more general reward response instead of specific to approach/avoid trials we also analyzed and compared to text feedback trials.

Second-level analyses employed a fixed-effects model in SPM12 implemented in MATLAB R2014a. All statistical maps were cluster-corrected with a mean cluster threshold of $Z > 4.95$ and a whole brain corrected cluster significance threshold of $p \leq 0.001$.

3. Results

3.1. Anticipation of social approval and avoidance of disapproval

In the anticipation phase we report several brain region activations located all across the brain involved in biological motion processing as well as an activation of the thalamus during the avoidance of negative motion feedback in contrast to negative text feedback (AVOI MOTION > AVOI TEXT) (Table 1) (Figure 5).

Table 1. Main and simple effects of factorial design during the anticipatory phase (ANT).

Region	BA	MNI Coordinates			Putative Functional Name	*t* value	Cluster size	$p_{corrected}$ value
		x	y	z				
(a) ANT APR MOTION > APR TEXT								
L angular gyrus	**39**	**-45**	**-55**	**34**	**AnG**	**6.00**	**127**	**<0.001**
		-45	-61	46		5.45		<0.001
		-39	-67	43		5.40		<0.001
(b) ANT APR > CONTROL (MOTION)								
R middle temporal gyrus	37	51	-61	10	MTG	5.85	130	0.001
		39	-61	7		4.71		0.001
		57	-58	1		4.50		0.001
R cuneus	**18**	**6**	**-88**	**22**	**Cun**	**5.54**	**483**	**<0.001**
		-9	-88	37		5.49		<0.001

		6	-82	28		5.28		<0.001
R postcentral gyrus	**4**	**45**	**-10**	**34**	**PoG**	**5.32**	**163**	**<0.001**
		60	-4	22		4.79		<0.001
		48	-19	28		4.73		<0.001
(c) ANT APR > CONTROL (TEXT)								
L precuneus	**5**	**-15**	**-52**	**70**	**PCu**	**8.09**	**206**	**<0.001**
		-3	-40	55		4.27		<0.001
		-21	-28	73		4.17		<0.001
R lingual gyrus	**18**	**18**	**-73**	**-5**	**LiG**	**7.11**	**1184**	**<0.001**
		-15	-70	-14		7.05		<0.001
		-15	-64	-2		6.32		<0.001
L middle temporal gyrus	**37**	**-54**	**-61**	**7**	**MTG**	**7.08**	**126**	**<0.001**
		-51	-79	16		4.75		<0.001
		-45	-67	22		4.16		<0.001
R precuneus	**5**	**15**	**-46**	**61**	**PCu**	**6.86**	**673**	**<0.001**
		18	-58	61		6.13		<0.001

		30	-46	58		5.57		<0.001
L postcentral gyrus	**3**	**-54**	**-13**	**34**	**PoG**	**6.71**	**173**	**<0.001**
		-48	-7	25		6.26		<0.001
		-54	-13	16		4.68		<0.001
L middle fronto-orbital gyrus	**11**	**-21**	**29**	**-14**	**MFO**	**6.04**	**184**	**<0.001**
(d) ANT AVOI MOTION > AVOI TEXT								
L lingual gyrus	**18**	**-18**	**-85**	**-8**	**LiG**	**5.49**	**131**	**<0.001**
		-6	-97	-5		5.17		<0.001
		-15	-97	7		4.81		<0.001
R thalamus		**3**	**-16**	**7**	**Th**	**5.36**	**148**	**<0.001**
		-15	-16	13		5.06		<0.001
		-15	-7	10		4.99		<0.001
(e) ANT AVOI > CONTROL (MOTION)								
R cuneus	**18**	**3**	**-85**	**22**	**Cun**	**8.19**	**2104**	**<0.001**

		-15	-58	-5		8.00		<0.001
		-6	-91	19		7.54		<0.001
R precuneus	5	12	-58	58	PCu	5.72	111	0.001
		27	-46	64		4.58		0.001
		33	-37	67		4.52		0.001
(f) ANT AVOI > CONTROL (TEXT)								
R lingual gyrus	**17**	**6**	**-76**	**-5**	**LiG**	**6.65**	**609**	**<0.001**
		-3	-79	-8		5.62		<0.001
		-9	-73	-8		5.32		<0.001

MNI coordinates of peaks of relative activation within regions responding to the main effects across conditions in the anticipation phase (approach motion vs approach text (a), approach motion vs control motion (b), approach text vs control text (c), avoid motion vs avoid text (d), avoid motion vs control motion (e) and avoid text vs control text (f). Results were calculated at $p_{\text{uncorrected}} < 0.001$, k = 10 voxels. Up to 3 local maxima are listed when a cluster has multiple peaks more than 8mm apart. Entries in bold denote activations significant at the *FDR* cluster-corrected level of $p < 0.001$. Only regions that reached cluster-corrected significance are illustrated in the figures. Abbreviations for brain regions: AnG = angular gyrus; MTG = middle temporal gyrus; Cun = Cuneus; PoG = postcentral gyrus; LiG = lingual gyrus; Th = thalamus; PCu = Precuneus; MFO = middle fronto-orbital gyrus.

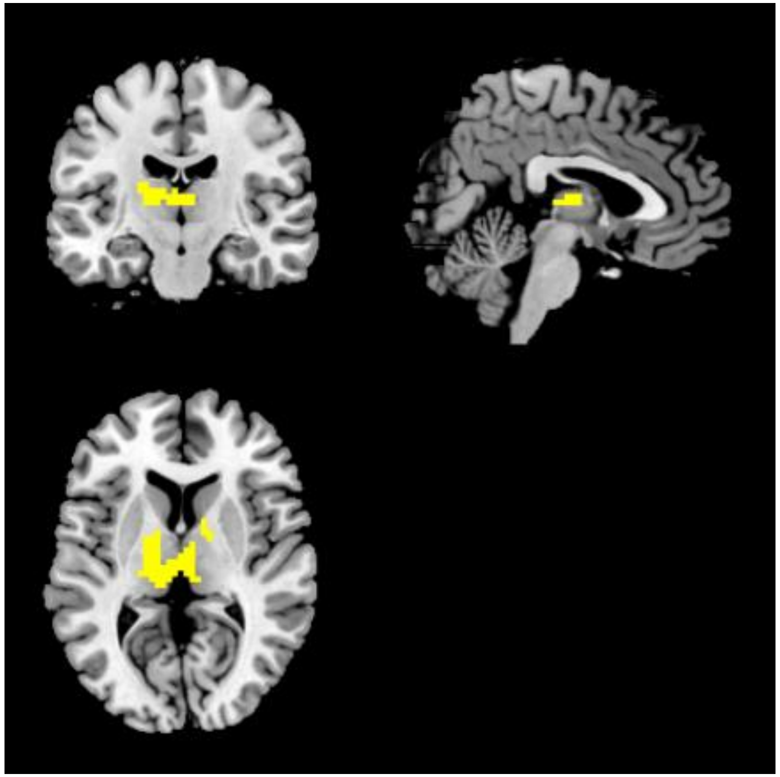


Figure 5. Thalamus activation (THAL; x = 3, y = -16, z = 7) seen in the anticipation phase AVOI MOTION vs AVOI TEXT condition, overlaid on the *Ch2bet* template in MNI space.

3.2. Behavioral correlations

Repeated measures ANOVA testing revealed a significant interaction between valence (reward/punishment), Wilks' Lambda = 0.967, F (1, 376) = 12930, p = 0.000, and valence x the Adult Autism Spectrum Quotient (AQ), Wilks' Lambda = 0.973, F (1, 376) = 10589, p = 0.001. Participants were significantly faster in the avoidment of punishment than for seeking reward in the motion condition (Figure 6). However, post-hoc t-test analysis revealed no significance in the valence x AQ interaction. Furthermore, no significant interactions were observed between the RT values of each participant per condition and each individuals' AQ values. Participants were also asked to rate the videos and text feedback before and after the task. The short clips were rated in a scale from 0 to 100, being 0 the most negative and 100 the most positive while 50 was defined as neutral. The scores before the task were used in order to determine which stimuli were going to be further used. No significant differences in scores were found between the ratings before and after the task. Moreover, accuracy was highly comparable across all conditions and remained consistent (~60% accuracy) (Figure 7).

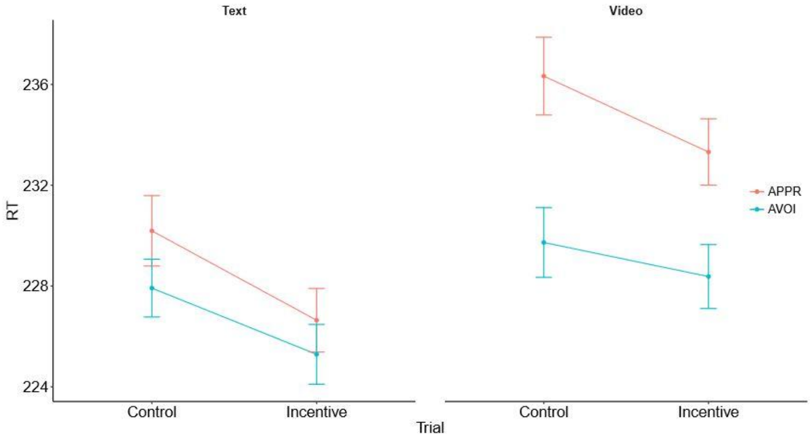


Figure 6. Graph of the mean RT times of participants. Red line depicts approach condition, blue line depicts avoidance condition.

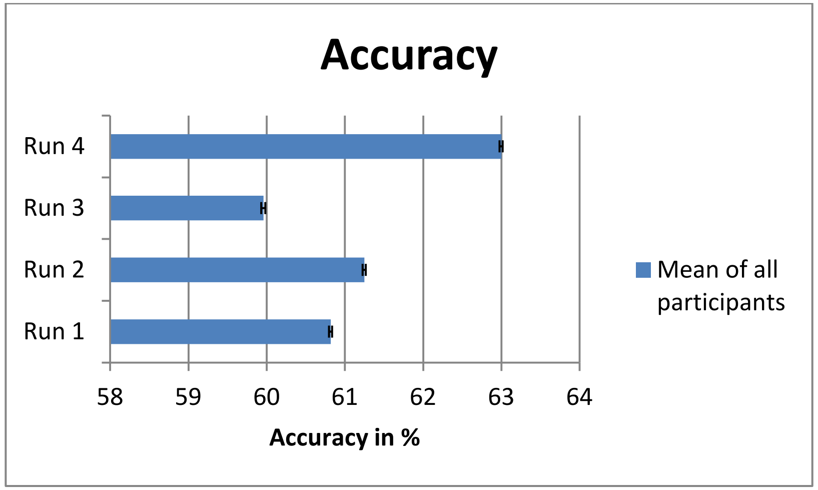


Figure 7. Graph of the mean accuracy percentage of all participants in each run. Average accuracy during run 1 was 60.82%, in run 2 61.25%, in run 3 59.96% and in run 4 63.00%. Thus, being the average of all runs 61.26%. Standard Error (SE) bars are shown: R1= 0.0199, R2= 0.0203, R3= 0.0261, R4= 0.0199. Standard Deviation (SD): R1= 0.1123, R2= 0.1148, R3= 0.1478, R4= 0.1128.

3.3. Outcome phase

Table 2. Main and simple effects of factorial design during the outcome phase (OUT).

Region	BA	MNI Coordinates x	y	z	Putative Functional Name	*t* value	Cluster size	$p_{corrected}$ value
(a) OUT APR MOTION > APR TEXT (HITS)								
L middle occipital gyrus	**19**	**-51**	**-73**	**4**	**MOcG**	**6.41**	**2541**	**<0.001**
		30	-61	-8		5.92		<0.001
		42	-79	-5		5.77		<0.001
R superior occipital gyrus	**19**	**27**	**-79**	**34**	**SOG**	**5.07**	**143**	**<0.001**
		18	-73	43		3.28		<0.001
R precentral gyrus	**6**	**45**	**2**	**52**	**PrG**	**4.30**	**360**	**<0.001**
		48	29	19		4.24		<0.001
		39	17	19		4.08		<0.001
R postcentral gyrus	**4**	**36**	**-34**	**49**	**PoG**	**4.14**	**127**	**<0.001**

		30	-49	52		3.89		<0.001
(b) OUT APR MOTION > APR TEXT (MISSES)								
L middle occipital gyrus	**19**	**-51**	**-73**	**4**	**MOcG**	**6.31**	**924**	**<0.001**
		-39	-82	7		5.25		<0.001
		-27	-55	-8		4.59		<0.001
R superior temporal gyrus	**42**	**63**	**-37**	**19**	**STG**	**4.02**	**120**	**<0.001**
		51	-37	16		3.96		<0.001
		57	-46	7		3.65		<0.001
(c) OUT APR > CONTROL (MOTION & TEXT HITS & MISSES)								
No superthreshold regions emerged from this analysis								
(d) OUT AVOI MOTION > AVOI TEXT								

(HITS)								
R inferior occipital gyrus		**42**	**-79**	**-5**	**IOG**	**5.36**	**516**	**<0.001**
		48	-58	4		5.07		<0.001
		48	-73	-2		5.03		<0.001
L middle occipital gyrus		**-48**	**-76**	**4**	**MOcG**	**5.13**	**332**	**<0.001**
		-30	-88	13		4.18		<0.001
		-18	-85	10		3.75		<0.001
(e) OUT AVOI MOTION > AVOI TEXT (MISSES)								
R middle temporal gyrus	**37**	**51**	**-67**	**4**	**MTG**	**5.86**	**932**	**<0.001**
		66	-31	19		5.05		<0.001
		27	-79	34		4.51		<0.001
L middle occipital gyrus	**19**	**-51**	**-76**	**4**	**MOcG**	**5.73**	**304**	**<0.001**
		-45	-61	10		4.99		<0.001
(f) OUT AVOI > CONTROL (MOTION & TEXT HITS & MISSES)								

No superthreshold

regions emerged from

this analysis

MNI coordinates of peaks of relative activation within regions responding to the main effects across conditions in the outcome phase (approach motion vs approach text HITS (a), approach motion vs approach text MISSES (b), approach vs control in both motion and text categories for both HITS and MISSES (c), avoid motion vs avoid text HITS (d), avoid motion vs avoid text MISSES (e) and avoid vs control in both motion and text categories for both HITS and MISSES (f). Results were calculated at $p_{\text{uncorrected}} < 0.001$, k = 10 voxels. Up to 3 local maxima are listed when a cluster has multiple peaks more than 8mm apart. Entries in bold denote activations significant at the *FDR* cluster-corrected level of $p < 0.001$. Only regions that reached cluster-corrected significance are illustrated in the figures. Abbreviations for brain regions: MOcG = middle occipital gyrus; SOG = superior occipital gyrus; PrG = precentral gyrus; PoG = postcentral gyrus; STG = superior temporal gyrus; IOG = inferior occipital gyrus; MTG = middle temporal gyrus.

4. Discussion

4.1. Anticipation of social approval and avoidance of disapproval

The present study aimed to observe if approving (reward) and disapproving (punishment) body motion would activate similar brain regions that have been found activated for monetary and facial rewads (i.e. ventral and dorsal striatum, nucleus accumbes, thalamus, and orbitofrontal cortex) compared to the text conditions (APR/AVOI MOTION > TEXT) as well as if body motion would elicit higher activation compared to controls (APR/AVOI > CONTROL) in reward-related brain regions, using a set of ecologically valid social stimuli (i.e. short video feedback instead of static images. We found strong activation ($p_{corrected} < 0.001$) of brain areas linked to higher motion processing and more specificaly, biological motion processing such as the lingual gyrus, cuneus, postcentral and middle temporal gyri (Servos, Osu, Santi & Kawato, 2002; Jung et al., 2009). More specifically, the lingual gyrus and the cuneus have been shown to be activated in speed discrimination tasks in comparison with simple motion detection task (Orban et al., 1998) as well as a far greater involvement of lingual gyrus than the MT/MST complex in motion direction discrimination tasks than in simple detection tasks (Cornette et al., 1998). These studies demonstrate that the same visual input and the same attribute (e.g. speed or direction of motion) produce different activation sites depending on whether or not a temporal comparison is required. Other studies have shown activation in the lingual gyrus during the observation of second-order motion compared with first-order motion (Smith, Greenlee, Singh, Kraemer & Hennig, 1998), and during the observation of motion-defined gratings, but not during the observation of static dots or unidirectional speed (Shulman, Schwarz, Miezin & Petersen, 1998). These findings are consistent with the role of the lingual gyrus in such higher-level motion processing. Moreover, the precuneus has been found to be active during unattended third-person perspective taking in social tasks. More specifically, these are tasks where the participant is just a passive spectator (unattended third person) watching a social interaction between other characters. In addition, it is thought to play a role in violations of social expectations (Petrini, Piwek, Crabbe, Pollick, & Garrod, 2014). Similarly, the angular gyrus is thought to compute action awareness and to be involved in awareness of action discrepancy and awareness of action authorship (Farrer et al., 2008). According to some authors it could, alternatively, reflect increased attentional processing of visual feedback (Desimone and Duncan, 1995).

The AVOI MOTION > TEXT condition in the anticipation phase revealed a significant cluster activation located in the thalamus, known for playing a role in the reward circuitry of the brain (Ikemoto, Yang & Tan, 2015; Kohls et al., 2013). Although many studies using the SID task to explore the reward system of the brain have found significant activations in important reward-associated regions such as the Nacc, VS, and the amygdala, we have not found any significant activations in those areas. These results were unexpected since they were part of our hypothesis, however we think it could partially be due to the stimuli not being rewarding enough to elicit activation. In a study by Demurie and colleagues (Demurie, Roeyers, Baeyens & Sonuga-Barke, 2012), the effects of anticipation of monetary and social rewards were compared in children and adolescents. Their experiment consisted on two tasks, the SID-plus, where points and written compliments were given as social rewards, and the SID-basic, where smiling faces and spoken compliments were used. Their results showed an effect of intensity: subjective value of the face-compliment combinations increased with increasing intensity of the faces' happiness and increasing compliment value. However, this intensity effect was not reflected in their behavioural data. In other words, reward anticipation had no effect on performance in the SID-basic social reward task. Therefore, it could be the case that our stimuli were not "strong" enough to elicit a change in the participants' behavior and by extension, their brain activation pattern. Other possibilities could involve the high number of females present in this study acting as a bias of results. It has been observed in several studies that there are gender-biases in response in reward-related decision processing tasks under stress conditions (Lighthall et al., 2012; Ossewaarde et al., 2011; Bogdan & Pizzagalli, 2006). Stressed females have been shown to have decreased activation in reward-related areas such as the dorsal striatum, insula, and medial prefrontal cortex compared to the males'.

In the SID task participants have to react as fast as possible to the target and the trials are repeated for a long time (in this study, 1 hour) which could have led to mild stress experienced by the participants. In addition, the experiment was conducted mostly with students from the University who could have been already stressed because of exams or projects regarding their studies. Some participants made verbal remarks about their studies' situation. Several studies have reported the alarmingly rise of numbers of university studients suffering from stress (Zascavage, Winterman, Buot, Wies, & Lyzinski, 2012; Saleh, Camart, & Romo, 2017) in the last five years. Since our analyses included a higher number of females than males and due to the nature of the task it could be a partial reason why no other reward-related areas showed as significant, except for the thalamus. Nonetheless, it is known that the thalamus plays an important role in dynamic and sensory processing via visual-related areas (Merabet, Desautels, Minville, & Casanova, 1998; Guillery, Feig, & van Lieshout, 2001; Rokszin et al., 2010). As some research has shown, reward system-related areas such as the striatum have been found to be recruited in greater amounts during avoidance of social punishment than seeking social reward and it's been correlated with social-related disorders such as social anxiety disorder (SAD) (Laricchiuta & Petrosini, 2014; Cremers et al., 2015; Richey et al., 2016) which shares some common social impairments with other disorders such as Autism and are often co-morbid (Bejerot, Eriksson, & Mörtberg, 2014; Maddox & White, 2015). Although no significant differences between RTs and the AQ have been found behaviorally, no further brain-behavior correlation tests have been performed due to time restrictions. Future reasearch testing the saliency of body motion videos as feedback and looking into the stress-brain-behavior relationship could help clarify how the reward system of the brain activates in response to positive and negative biological motion as feedback.

Finally, the live-action feedback footage resulted in more BOLD activation throughout visual-processing areas (e.g. lingual gyrus, cuneus) and subcortical sensory pathways (thalamus). These early visual areas are sensitive to cues of perceptual depth (Backus, Fleet, Parker, & Heeger, 2001), and the live-action feedback certainly presented more information compared to the text feedback, which may have appeared flat in comparison. Subcortical sensory pathways may have been more activated by the greater information contained within the live-action video segments. The orbitofrontal region is most often associated with reward, with the anterior portion responding to even quite abstract reinforcers such as music (Kringelbach, 2005). Our finding of activation in this region correspond to the anterior orbitofrontal gyrus, and may indicate that positive text feedback was viewed as more rewarding and thus, elicited activation during the anticipation of positive feeback compared to control feedback.

4.2. *Behavioral correlations*

Repeated measures ANOVA testing revealed a significant interaction between valence (reward/punishment), Wilks' Lambda = 0.967, F (1, 376) = 12930, p = 0.000, and valence x the Adult Autism Spectrum Quotient (AQ), Wilks' Lambda = 0.973, F (1, 376) = 10589, p = 0.001. Participants were significantly faster in the avoidment of punishment than for seeking reward in the motion condition (Figure 7). This, along with the Thalamus activation on the AVOI MOTION > TEXT seems to indicate that avoidment of punishment is at least just as rewarding, if not more, than seeking reward. This line of thought correlates with the results seen in Kohls et al., 2013. However, post-hoc t-test analysis revealed no significance in the valence x AQ interaction. Furthermore, no significant interactions were observed between the RT values of each participant per condition and each individuals' AQ values. Although, these results may come as surprising since the Social Motivation Theory hints at possible behavioral response differences to social cues it is not contradictory with it as these statistical tests were performed on behavioral measures only (RTs x AQ) and as seen in several studies, behavioral outcomes do not always match imaging brain patterns (Dichter et al., 2012), thus further ROI analyses and brain-behavioral correlation tests will have to be performed in order to determine if any significant differences can be seen in the brain correlating valence (reward/punishment trials) to AQ.

Participants were also asked to rate the videos and text feedback before and after the task. The short clips were rated in a scale from 0 to 100, being 0 the most negative and 100 the most positive while 50 was defined as neutral. The scores before the task were used in order to determine which stimuli were going to be further used. No significant differences in scores were found between the ratings before and after the task. Therefore, it can be assumed that participation in the task had no effect in their ratings about how positive or negative they found the stimuli to be.

Finally, the task was designed with a staircase design with the purpose of maintaining the participants' accuracy stable at ~60% hit rate. Accuracy was thus highly comparable across all conditions and remained consistent.

4.3. Outcome phase

Output phase was modelled separating HIT trials and MISS trials since animal research has shown that VS/Nacc signals to reward-predicting cues are significantly greater when subsequent operant responses to the cues are accurate (i.e. hit) rather than inaccurate (i.e. miss) (Francois et al., 2012; Nicola et al., 2004). Occipital and temporal areas were found to be active (Brodmann areas: 19, 37, 42) which is consistent with literature reporting those areas to be involved in biological motion perception and recognition (Vaina, Solomon, Chowdhury, Sinha, & Belliveau, 2001; Saygin, 2007). All conditions comparing motion and text (APR/AVOI MOTION > TEXT) showed significant activation of these areas. On the other hand, conditions comparing incentive feedback to the control feedback (APR/AVOI MOTION/TEXT > CONTROL) did not show significant activation of any brain areas, neither in the hit trials nor the miss ones.

5. Conclusion

In this novel study we found significant activation of biological motion-specific areas as well as a significant activation of the thalamus in the anticipation phase of AVOI MOTION > AVOI TEXT, meaning participants may have found avoiding negative motion feedback more rewarding than avoiding negative text feedback. In addition, we have found an overall activation of areas specifically related to biological motion. The thalamus activation observed in the anticipation phase of approach motion vs text may hint to biological motion being more rewarding than text feedback. All together these results provide initial evidence of specialized biological motion brain areas being activated in response to video stimuli as feedback. However, as this is a novel study exploring the rewarding value of biological motion by using dynamic stimuli as feedback, future measures must be taken correcting for this study's limitations such as the stimuli possibly not being "strong" enough to elicit brain reward system activation and the lack of a diagnosed ASD group. Future research will be necessary to clarify whether biological motion elicits similar activation of the reward system as faces or money do.

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