Brain Imaging and Behavior
https://doi.org/10.1007/s11682-019-00215-3

ORIGINAL RESEARCH

Basal ganglia lateralization in different types of reward

Marie Arsalidou[1,2] · Sagana Vijayarajah[3] · Maksim Sharaev[4]

Abstract

Reward processing is a fundamental human activity. The basal ganglia are recognized for their role in reward processes; however, specific roles of the different nuclei (e.g., nucleus accumbens, caudate, putamen and globus pallidus) remain unclear. Using quantitative meta-analyses we assessed whole-brain and basal ganglia specific contributions to money, erotic, and food reward processing. We analyzed data from 190 fMRI studies which reported stereotaxic coordinates of whole-brain, within-group results from healthy adult participants. Results showed concordance in overlapping and distinct cortical and sub-cortical brain regions as a function of reward type. Common to all reward types was concordance in basal ganglia nuclei, with distinct differences in hemispheric dominance and spatial extent in response to the different reward types. Food reward processing favored the right hemisphere; erotic rewards favored the right lateral globus pallidus and left caudate body. Money rewards engaged the basal ganglia bilaterally including its most anterior part, nucleus accumbens. We conclude by proposing a model of common reward processing in the basal ganglia and separate models for money, erotic, and food rewards.

Keywords Rewards · fMRI · Meta-analyses · Striatum · Basal ganglia

The prospect of reward is a significant motivator in all species. Both animals and humans modulate their behavior to achieve potential rewards. External factors such as the perceived value, contextual circumstances and reward quantity can influence how individuals approach rewarding situations (Green and Myerson 2004). Importantly, examining both the behavioral and neural mechanisms that support reward behavior will further our understanding of the decision-making, reasoning, and introspection processes that impact our reward motivated behaviors. Past work on the neural mechanisms that support reward processing have found basal ganglia—a cluster of gray matter nuclei located at the base of the forebrain—respond to monetary (Hardin et al. 2009), erotic (Kim et al. 2006), and food (Grabenhorst et al. 2010) rewards. A recent functional magnetic resonance imaging (fMRI) meta-analysis suggests there is variability in hemispheric lateralization in rewards tasks (Arsalidou et al. 2013), however, a direct test of this lateralization across reward types has not been reported. Specifically, despite increased interest in the basal ganglia's role in reward processes, the hemispheric and spatial extent of these reward processing contributions within basal ganglia *nuclei* remains unclear. The purpose of the current project was to compile fMRI studies that examine money, erotic, and food reward processing, and identify over-arching patterns across studies that will be used to provide a stereotaxic atlas of basal ganglia reward processing in healthy adults.

Biological rewards such as food and mating are sought by both animals and humans. Considering the cross-species importance of food and mating, such rewards have been classified as primary rewards. Studies investigating the neural correlates of food consumption have identified that the limbic system (including the basal ganglia) are associated with the anticipation of food (Stice et al. 2013) and food intake (van Bloemendaal et al. 2015). Similar to food rewards, erotic rewards also activate the basal ganglia, (Chowdhury et al. 2013; Jansma et al. 2013; Lawrence et al. 2012).

However, not all reward seeking behaviors are motivated by biological necessities. Stemming from society-based importance, secondary rewards such as wealth and prestige can

✉ Marie Arsalidou
marie.arsalidou@gmail.com

1 Department of Psychology, National Research University Higher School of Economics, Moscow, Russian Federation

2 Department of Psychology, Faculty of Health, York University, Toronto, ON, Canada

3 Department of Psychology, Faculty of Arts and Science, University of Toronto, Toronto, ON, Canada

4 Skolkovo Institute of Science and Technology, Moscow, Russian Federation

Published online: 11 January 2020

hold substantial value. Studies on the brain regions associated with monetary reward have shown that prefrontal and lateral frontal regions, as well as subcortical structures such as the basal ganglia and amygdala have been linked to secondary reward valence and decision making (Elliott et al. 2004), and are implicated in rapidly processing monetary anticipation, gain, and loss (Gehring and Willoughby 2002; Elliott et al. 2004). Some studies report that the right ventral striatum and caudate are associated with reward valance (Waltz et al. 2010), whereas other studies suggest that the left ventral striatum (Elliott et al. 2000; Weil et al. 2010) or all bilateral basal ganglia sub-nuclei (Knutson et al. 2001) are associated with monetary reward. Critically, these money processing regions are also implicated in tasks that incorporate complex decision-making (Christoff et al. 2009), suggesting that these and other regions may potentially be crucial to reward outcome processing that occurs after decision-making processes. Furthermore, the incomparable experimental paradigms used by these studies may explain conflicting findings in the reward literature, and highlight the need for second-order analyses of the data to identify over-arching patterns across studies.

Past meta-analyses have examined the effects of valence in reward processing (Liu et al. 2011), whether the reward is personal or vicarious (Morelli et al. 2015), and how reward processing relates to decision making (Diekhof et al. 2008), in teenagers (Silverman et al. 2015), individuals diagnosed with schizophrenia (Leroy et al. 2015; Schlagenhauf et al. 2008), obesity, and substance addiction (García-García et al. 2014). Knowledge contributions of these meta-analyses are focused mainly on monetary rewards and do not distinguish among the different reward types that motivate human behavior (i.e., monetary, erotic, and food). A meta-analysis by Sescousse et al. (2013) is the only meta-analysis that effectively captured the broad processing of both primary and secondary rewards. Using 87 studies on monetary, erotic, and food incentives, separate analyses on the different forms of reward and their shared activation were performed. Whole-brain results showed that ventral bilateral basal ganglia, bilateral anterior insula/frontal operculum, mediodorsal thalamus, bilateral amygdala, and the region extending between the ventromedial prefrontal cortex into the pregenual anterior cingulate cortex shared overlapping activation for all three reward types (Sescousse et al. 2013).

Although the critical role of the basal ganglia is recognized, the specific hemispheric contributions of each nucleus remains uncertain. While previous findings have demonstrated that executive processes (i.e. decision making) were right lateralized in the caudate head and reward processes left lateralized in the caudate body (Arsalidou et al. 2013), important distinctions among nuclei and laterality have not been distinguished among primary versus secondary reward types. Furthermore, it is unclear how the reward processing organization of the basal ganglia nuclei interact with the rest of the brain. A primary purpose of the current project was to identify distinct and common hemispheric contributions of the basal ganglia nuclei in fMRI studies that examined the reward processes outcomes to monetary, food, and erotic stimuli in humans.

Methods

Literature search and article selection

Three searches for human studies on monetary, food and erotic rewards published between July 2010 and June 2016 were performed using the PubMed search engine; keywords (money OR monetary OR financial) AND reward AND (fMRI OR PET OR neuroimaging); (food OR taste OR juice) AND (reward OR pleasant) AND (fMRI OR PET OR neuroimaging); (erotic OR sexual) AND (stimuli) AND (fMRI OR PET OR neuroimaging). To retrieve the studies included in Sescousse et al. (2013), the three searches were replicated for studies published before July 2010. One food and erotic article included in Sescousse et al. (2013) could not be retrieved (Domenech and Dreher 2008 was a conference paper). We did not consider unpublished data. Critically, although we retrieved PET studies, we chose not to include them in the analyses to minimize confounds related to the imaging methodology. While Sescousse et al. (2013) included PET studies—likely due to a smaller sample of studies present at the time—our updated search retrieved a sufficient sample of fMRI studies but not enough PET studies that met our criteria for each reward type were available to be analyzed separately ($n = 10$). Although findings we report here consider only fMRI studies, we did perform the analyses combining both fMRI and PET studies; results showed that concordant regions were comparable. Figure 1 enumerates the identified articles and subsets of those that remained after screening for our eligibility criteria.

Specifically, we used the eligibility criteria described here when selecting our final sample. (1) To ensure that analyses were not biased by a priori regions-of-interest, only studies that included contrasts (i.e., experiments) from whole-brain random-effects analyses were included. (2) Only studies that reported activation foci in either Talairach or Montreal Neurological Institute (MNI) standardized stereotaxic space were selected. (3) To assess activation associated with healthy adult reward processing outcomes, the articles selected included experiments with healthy, drug-free, adult participants and reported within-group contrasts associated with reward outcome. Therefore, to minimize variability associated with other reward/non-reward processes, studies that only reported contrasts for reward anticipation or included stimuli that were not subjectively rewarding were excluded. The food studies selected consisted of the participant receiving real food or juice

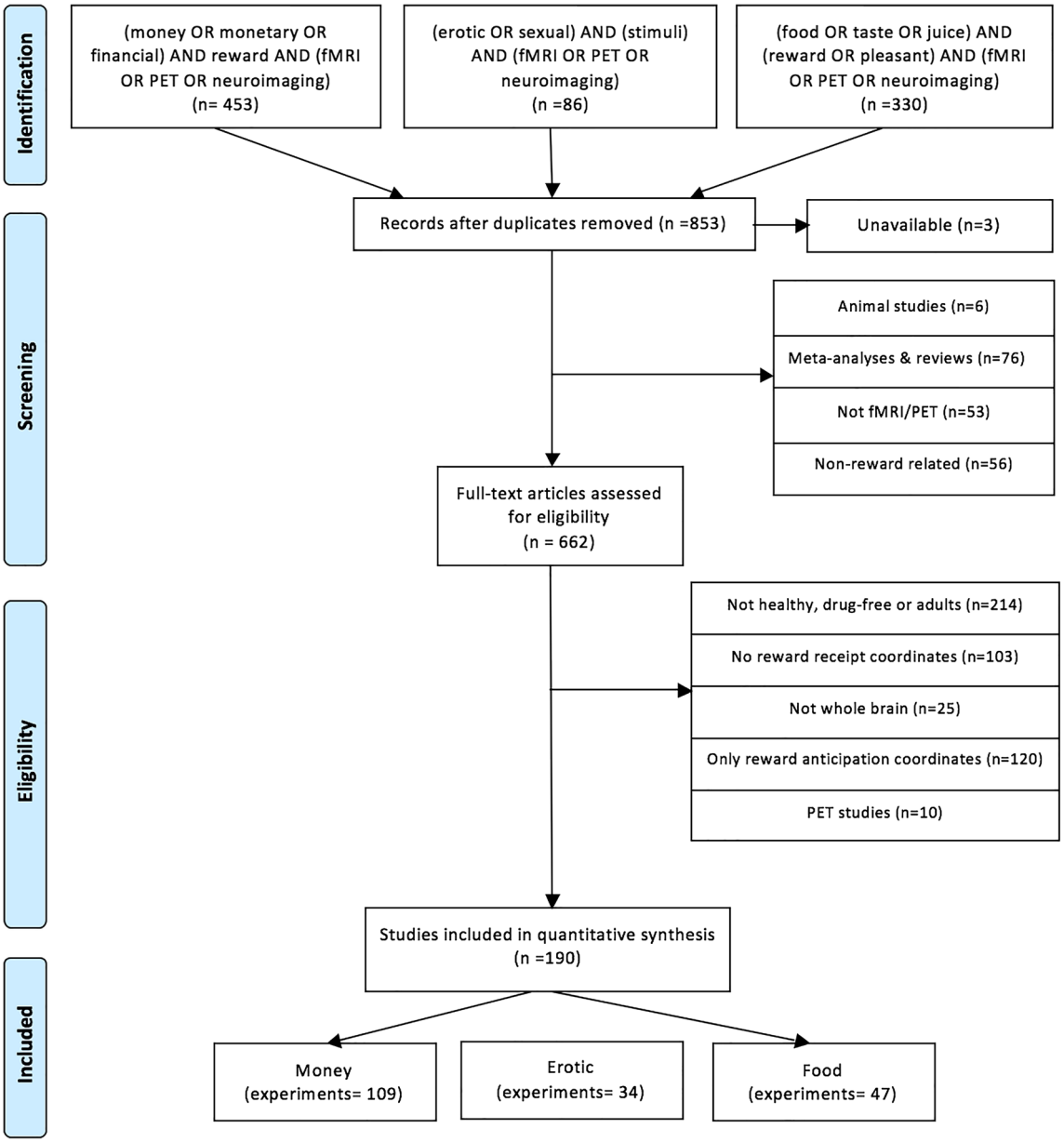

Fig. 1 PRISMA flowchart for processing steps taken for the identification and eligibility of articles (template by Moher et al. 2009). n = number of articles.

rewards. Erotic studies were included if they presented pictures or movies of sexually arousing stimuli. (4) If a study included more than one reward outcome contrast or provided many datasets for the three reward types, only one contrast per study was selected (i.e., the first reward outcome contrast listed). Although the current algorithm for computing concordance across studies controls for multiple experiments (i.e., contrasts) from the same paper (Turkeltaub et al. 2012), we selected a conservative approach for experiment selection as the number of experiments in each category was well over the currently recommended threshold of 17–20 experiments (Eickhoff et al. 2016; Eickhoff et al. 2009). After screening articles using our eligibility criteria, our meta-analyses included data from fMRI studies with monetary ($n = 109$ experiments; $n = 1132$ foci; Table 1), erotic ($n = 34$ experiments; $n = 570$ foci; Table 2), and food ($n = 47$ experiments; $n = 535$ foci; Table 3) rewards.

Meta-analyses

We used Activation Likelihood Estimation (ALE; version 3.0.2), a coordinate-based meta-analysis method provided through BrainMap (Eickhoff et al. 2009; Turkeltaub et al. 2002) that uses a random-effects analysis to assess clustering. All MNI coordinates were transformed into Talairach space using the Lancaster transform function. Talairach contrast

Table 1 Characteristics of the monetary studies included in the meta-analyses

Article	n	Age	Foci	Handedness	TR (sec)	Field strength (T)	Task	Contrast
Abe et al. (2014)	28 (10 males)	23.1 years	6	right	2.5	3	MID	Win > no win
Abler et al. (2007)	8 (4 males)	31.3 (± 8.8 years)	10	right	1.5	3	MID	Placebo: win > omission
da Silva Alves et al. (2011)	10 (10 males)	18–40 years	6	right	2	3	MID	Placebo: reward > no outcome & loss
Andrews et al. (2011)	49 (17 males)	33.7 ± 13.8 years	3	right	1.5	3	MID	Reward > loss
Aoki et al. (2014)	20 (12 males)	20.8 ± 1.3 years	7	n/a	2.5	3	MID	Reward outcome > loss outcomes
Barman et al. (2015)	63 (32 males)	23.5 ± 2.2 years	6	n/a	2.5	3	MID	Monetary > social reward feedback
Bjork et al. (2004)	12 (6 males)	23.8 (± 2.0 years)	16	right	2	3	MID	Gain > no gain outcome
Bjork et al. (2008)	23 (12 males)	32. 0 (± 8.0 years)	5	right	2	3	MID	Reward > failure to win reward
Bjork et al. (2010)	24 (12 males)	29.3 (± 5.7 years)	7	right	1	3	MID	Reward > non-reward notification
Bjork et al. (2012)	23 (12 males)	30.1 ± 5.9 years	7	right	1	3	MID	Reward > no reward
Boecker et al. (2014)	162 (68 males)	24.4 years	5	n/a	2.2	3	MID	Win > no win trials
van den Bos et al. (2013)	22 (11 males)	28.6 ± 7.3 years	3	n/a	2	3	Auction Task	Outcome: win > no win
Bothe et al. (2013)	48 (48 males)	20–30 years	6	right	2	1.5	MID	Gan > no gain
Braams et al. (2014)	31 (12 males)	20.9 ± 2.0 years	5	right	9.7	3	Ultimatum Game	Main effect of reward outcome
Bustamante et al. (2014)	18 (18 males)	37.4 ± 8.2 years	3	right	11	1.5	MID (modified)	Reward > non-incentive cues
Camara et al. (2008)	17 (7 males)	21.6 (± 2.6 years)	18	right	2	3	Gambling Task (modified)	Gain (5 + 25) > fixation
Camara et al. (2010)	655 (164 males)	21.7 ± 3.5 years	3	n/a	2	3	Gambling Task (modified)	Gain (5 + 25) > loss (5 + 25)
Carlson et al. (2011)	45 (27 males)	21.1 ± 1.3 years	15	40 right, 5 left	2.5	3	Gambling Task	Reward > loss
Causse et al. (2013)	15	25.4 ± 2.5 years	6	right	2.4	3	Decision-Making Task	Financial > neutral incentive
Choi et al. (2014)	20 (8 males)	27.9 ± 4.6 years	66	right	1.9	3	MID (modified)	Reward > threat
Chowdhury et al. (2013)	42 (13 males)	69.1 ± 3.4 years	3	40 right, 2 left	2.37	3	Go/No-Go (modified)	Win > loss
Clark et al. (2009)	15 (9 males)	26.0 (± 7.5 years)	18	right	2	3	Slot Machine Task	All winning > all non-win outcomes
Clithero et al. (2011)	16 (16 males)	23 years	3	n/a	2	3	Incentive Compatible Task	Money > face
Cox et al. (2005)	22 (12 males)	18–30 years	28	right	3	3	Conditioning Reward Task	Reward > negative feedback
Dowd et al. (2012)	20 (14 males)	33.2 ± 9.4 years	22	n/a	2	3	Pavlovian Prediction Task	Money > no money
Elliott et al. (2000)	9	n/a	2	n/a	n/a	2	Card Game	Positive correlation of reward level
Elliot et al. (2003)	12 (6 males)	23.6 years	12	right	5	1.5	Target Detection Task	Reward > non- rewarded responses
Elliott et al. (2004)	12 (6 males)	23.6 years	10	right	5	1.5	Target Detection Task	Main effect of reward
Ernst et al. (2005)	14	20–40 years	12	right	2	3	Wheel of Fortune Gambling Task	Monetary outcomes > no reward
Fareri et al. (2012)	20 (10 males)	20.5 ± 2.2 years	6	n/a	2	3	Gambling Task	Positive > negative outcomes
Fareri et al. (2014)	18 (10 males)	20.4 ± 2.2 years	18	n/a	2	3	Card-Guessing game	Main effect of reward outcome
Fauth-Bühler et al. (2014)	89 (89 males)	36.2 ± 9.4 years	1	right	2.41	3	Modified Instrumental-Motivation Task	Reward > loss feedback
Figee et al. (2011)	19 (6 males)	32.0 ± 6.6 years	10	right	19.23	1.5	MID (modified)	Receipt of reward > no reward.
Filbey et al. (2013)	27 (4 males)	30.32 ± 10.1 years	12	right	2	3	MID	Gain > neutral
Fujiwara et al. (2009)	17 (12 males)	20–29 years	18	right	2	1.5	Card Game	Gain-specific regions
Furl et al. (2011)	18	n/a	8	right	2	3	Matching Urn Guessing Task	Urn > draw choices
Gossen et al. (2014)	35 (35 males)	23.5 ± 2.3 years	3	right	2.2	3	MID and Social Delay Task	Money > social reward
Hardin et al. (2009)	18	29.0 ± 4.8 years	7	right	2	3	Wheel of Fortune Gambling task (modified)	Gain outcomes > loss outcomes
Hasler et al. (2013)	113 (113 males)	20 years	3	n/a	2	3	Card Guessing Task	Win > loss
Hasler et al. (2014)	11 (4 males)	21.5 ± 1.7 years	4	n/a	2.2	3	Card Guessing Task	Gain > baseline

Table 1 (continued)

Article	n	Age	Foci	Handedness	TR (sec)	Field strength (T)	Task	Contrast
Hausler et al. (2015)	33 (33 males)	24.4 ± 3.2 years	6	n/a	2.5	n/a	Incentive Task	Win > no win
Hawes et al. (2014)	94 (94 males)	18–38 years	4	right	2	3	Outcome Prediction Task	Gain > loss feedback
Hermans et al. (2010)	12 (0 males)	20.4 years	15	right	3.4	3	Incentive Task (modified)	Reward > loss
Izuma et al. (2008)	19 (9 males)	21.6 ± 1.5 years	23	right	3	3	Gambling Task	High monetary > no monetary reward
Kahnt et al. (2014)	30 (15 males)	24.0 ± 0.6 years	8	right	2	3	Non-Instrumental Outcome Prediction Task	Reward salience: gain > loss
Kanayet et al. (2014)	16 (7 males)	22.2 years	8	right	2.1	3	Lottery Task	Activation positively associated with numeric magnitude
Katahira et al. (2015)	25 (13 males)	24.4 ± 5.3 years	10	n/a	7.32	3	Decision Task	Gain > no gain
Kim et al. (2011)	18 (8 males)	26.5 ± 4.94 years	3	right	2	3	MID (modified)	Money > loss outcome
Kim et al. (2015)	19 (10 males)	Males: 25.5 ± 3.0 Females: 23.4 ± 1.7	6	right	2	3	Fractal Probability Task	Rewarded > neutral
Kirk et al. (2015)	78 (23 males)	Controls: 36.5 ± 9.7 years Meditators: 40.2 ± 10.3 years	5	n/a	2	3	MID (modified)	Gain > non-gain
Knutson et al. (2001)	9 (2 males)	26.5 ± 5.9 years	6	right	2	1.5	MID	Reward > non-reward trials
Knutson et al. (2003)	12 (6 males)	31 years	4	right	2	1.5	MID	Gain > no outcome
Knutson et al. (2008)	12 (4 males)	28.7 ± 4.3 years	16	Edinburgh Handedness Inventory Score: mean = 37.11	2	1.5	MID	Gain > no outcome
Koch et al. (2014)	42 (17 males)	25.5 ± 5.2 years	15	right	2.04	3	Probability Guessing Task	Monetary win > monetary loss
Koester et al. (2013)	15 (9 males)	26.5 ± 4.2 years	2	n/a	2	3	Decision-Making Gambling Task	Experimental > control
Kohno et al. (2015)	60 (33 males)	18–51 years	5	right	2	3	Balloon Analogue Risk Task	Cashing out an active balloon
Kokal et al. (2011)	18 (0 males)	23.0 years	24	right	1.5	3	Gambling Task	High monetary reward > no monetary
Kumar et al. (2014)	18 (7 males)	31.7 ± 12.3 years	6	right	2.5	1.5	MID	Reward > no-incentive cue
Kurniawan et al. (2010)	18 (5 males)	27.0 ± 3.0 years	1	right	2.72	3	Monetary Choice Task	Reward > grip
Kurniawan et al. (2013)	19 (11 males)	21.7 ± 2.7 years	3	right	3.36	3	Probabilistically Reward Task	(win – neutral in winning trials) > (neutral – loss in losing trials)
Hernandez Lallement et al. (2014)	30 (16 males)	25.4 ± 4.0 years	1	right	2.5	1.5	Calculation Task	Modulation of BOLD signal by the amount of money
Lawson et al. (2014)	23 (15 males)	26.0 ± 4.48	20	n/a	3.2	3	Conditioning Task	Win value > loss
Li et al. (2013)	23 (16 males)	22.8 ± 1.6 years	13	n/a	2	3	Delay Discounting Task	Positive correlation with money magnitude
Lighthall et al. (2012)	47 (24 males)	Males: 23.0 ± 3.6 years Females: 21.8 ± 3.6 years	50	right	2	3	Balloon Analogue Risk Task	Active > passive
Lin et al. (2012)	22 (0 males)	22.4 years	15	right	2	3	Slot Machine Task	Monetary outcome > baseline
Linke et al. (2010)	33 (17 males)	22.6 ± 2.9 years	16	right	2.7	3	Probabilistic Reversal Learning Card Task	Reward > punishment
Luo et al. (2012)	21 (8 males)	29.9 ± 6.1 years	5	right	2	3	Delay Discounting Task	Positive association with subjective value of reward

Table 1 (continued)

Article	n	Age	Foci	Handedness	TR (sec)	Field strength (T)	Task	Contrast
Martin et al. (2009)	20	19.6 ± 1.35 years	2	n/a	2.5	3	Conditioning Task	Reward > no reward
Martin et al. (2011)	30 (15 males)	20.9 ± 3.0 years	18	right	2	3	Conditioning Task	Reward receipt magnitude
Martin et al. (2014)	17	n/a	2	right	2	3	Reward Prediction Task (modified)	Non-smokers gains > losses
Martin-Soelch et al. (2011)	24 (12 males)	20–46 years	8	right	n/a	1.5 and 3	Slot Machine Task	Win > no win
Mowrer et al. (2011)	34 (16 males)	23.5 years	10	right	2.2	3	Conditioning Task	Monetary outcome > control
Mullin et al. (2013)	27 (11 males)	23.1 ± 1.6 years	4	right	2	3	Card Guessing Task	Reward > loss
Murayama et al. (2010)	28 (10 males)	20.6 ± 1.1 years	9	right	2.5	3	Stopwatch Task	Success > failure
Nieuwenhuis et al. (2005)	14 (8 males)	25.4 years	10	right	2	1.5	Card Task	+$60 > $0
O'Connor et al. (2012)	18 (9 males)	23.0 years	19	right	2	3	Go/No-Go	Successful > unsuccessful no-go trials
O'Doherty et al. (2003)	15 (5 males)	N/A	7	right	2.78	2	Choice Reversal Task	Reward > punishment
Ossewaarde et al. (2011a)	19 (9 males)	24.6 ± 7.1 years	15	right	2.34	1.5	MID (modified)	Reward > non-reward
Ossewaarde et al. (2011b)	29 (0 males)	18–25 years	12	right	1.89	3	MID	Reward > non-reward
Ossewaarde et al. (2011c)	28 (0 males)	22.8 years	15	right	1.89	3	MID	Reward > non-reward
Petrovic et al. (2008)	13 (13 males)	24 years	11	right	3.96	1.5	Gambling Task	Reward > zero block
Ramnani et al. (2004)	6	n/a	6	n/a	2.48	2	Conditioning Task	Unexpected reward outcomes > baseline
Reuter et al. (2005)	12 (12 males)	32.3 ± 5.6 years	4	right	2.2	3	Guessing Task	Main effect of winning > main effect of losing
Ripke et al. (2012)	28 (15 males)	25.0 ± 5.8 years	14	n/a	2.41	3	Intertemporal Choice Task	Adults: subjective value of reward > baseline
Rogers et al. (2004)	14 (9 males)	23.4 ± 1.4 years	12	right	2	3	Decision-Making Gambling Task	Gain > loss
Rohe et al. (2012)	59 (37 males)	26.8 ± 4.2 years	6	n/a	2.5	1.5 and 3	Reward probability Task	Reward receipt > zero reward
Rudorf et al. (2014)	22 (16 males)	22.0 ± 2.5 years	16	right	2.46	3	Conditioning Task	Bonus > shape choices
Samanez- Larkin et al. (2010)	54 (28 males)	51.3 years	6	n/a	2	1.5	Behavioral Investment Allocation Strategy Task (modified)	Gain > loss outcomes
Sescousse et al. (2010)	18 (18 males)	24 ± 3.3 years	5	right	2.5	1.5	MID	Monetary reward outcomes > control
Seymour et al. (2012)	16	n/a	4	n/a	n/a	1.5	Probabilistic Instrumental Learning Task	Reward > punishment
Shigemune et al. (2014)	30 (8 males)	20.7 years	7	right	2	3	Encoding and Retrieval Task	Reward > control / punishment
Skvortsova et al. (2014)	20 (9 males)	24.0 ± 2.8 years	6	right	2	3	Probabilistic Instrumental Learning Task	Reward > effort
Smith et al. (2010)	23 (23 males)	21.8 years	10	n/a	2	3	Multimodal Reward Task	(+$5 & + $2) > (−$5 & -$2)
Speer et al. (2014)	26 (7 males)	20.0 ± 3.0 years	11	right	2	3	Card-Guessing Game	Gain > loss
Staudinger et al. (2011)	24 (11 males)	25.1 ± 2.8 years	6	right	1.65	3	MID (modified)	Reward > no reward
Suzuki et al. (2011)	17 (12 males)	21.4 ± 1.5 years	14	n/a	2	3	Prisoner's Dilemma Game	Payoffs > loss
Urban et al. (2012)	15 (8 males)	28.6 ± 5.5 years	4	n/a	1.5	3	MID	Reward > no reward
Vaidya et al. (2013)	18 (9 males)	27.7 ± 1.4 years	15	right	2	3	MID (modified)	Adults: gain > failure
van Leijenhorst et al. (2010)	15 (8 males)	20.2 ± 1.6 years	4	right	2.5	3	Slot Machine Task	Reward > reward omission
Varnum et al. (2014)	15 (5 males)	19–24 years	10	right	2	3	Card-Guessing Task	Win > loss
Van Der Vegt et al. (2013)	12 (5 males)	60.0 ± 7.0 years	14	n/a	2.5	3	Gambling Task	Reward outcome > loss
Völlm et al. (2007)	14 (14 males)	27.1 ± 7.1 years	19	right	5	1.5	Epoch Design Reward Task	Reward > non- reward blocks

Table 1 (continued)

Article	n	Age	Foci	Handedness	TR (sec)	Field strength (T)	Task	Contrast
Votinov et al. (2015)	60 (31 males)	23.8 ± 5.4 years	28	right	1.8	3	MID (modified)	Gain > loss
Weil et al. (2010)	12 (7 males)	20–32 years	8	right	2.4	3	Temporal Discrimination Reward Task	Reward > no reward
Weis et al. (2013)	39 (21 males)	24 years	25	right	1.5	3	Instrumental Learning Task	Reward > no reward
Wilbertz et al. (2012)	28 (14 males)	36.7 ± 9.3 years	8	right	2.25	3	Card-Guessing Task	Win > loss
Wimmer et al. (2014)	30	22 years	1	n/a	2	3	Reward Learning and Memory Task	Memory and reward interaction
Wu et al. (2014)	52 (23 males)	50 ± 16.5 years	20	right	2	1.5	MID	Gain > non-gain
Ye et al. (2011)	16 (16 males)	25 years	31	right	2	1.5	MID	Reward > non-reward outcome

coordinates of activation from eligible reward studies were combined to create 3D maps depicting the likelihood of activation within each voxel in an MRI template. Significant areas were identified depending on whether the reward processing location was more likely to occur in comparison to random spatial distributions. Analyses were thresholded using a cluster level correction for multiple comparisons at $p = 0.05$ with cluster forming threshold at $p = 0.001$ (Eickhoff et al. 2016). Contrast analyses were performed to identify common (i.e., conjunction) and significantly different brain areas involved in money, erotic, and food reward types. Since the contrast analyses used ALE maps thresholded for multiple comparisons, the threshold was set to uncorrected $p = 0.01$ (10,000 permutations, 200 mm^2 minimum volume for contrasts; Arsalidou and Pascual-Leone 2016; Yalpe and Arsalidou 2018). With these options, GingerALE software allows for between group comparisons, however, currently there are no options for correlational analyses (e.g., reward processes as a function of age).

Our regions of interest: nucleus accumbens, caudate head, caudate body, putamen, lateral globus pallidus and medial globus pallidus (Fig. 2) were defined using the TT:Deamon anatomical templates using AFNI (Cox 1996). The anatomical masks were applied to the thresholded ALE maps. Laterality indices [LI = (R-L)/(R + L)] were calculated using the proportion of suprathreshold voxels in each region. LI < −0.20 was deemed left dominant, LI > 0.20 was deemed right dominant and values in between were considered bilateral (Arsalidou et al. 2013).

Results

A total of 5551 participants took part in these studies. Tables 1, 2, and 3 show the participant characteristics (e.g., age, gender, and handedness) for studies that reported them. Overall, 3617 adults (49% male; average age: 27 years) participated in monetary tasks; 908 adults (71% male; average age: 27 years) participated in erotic tasks; 1026 adults (31% male; average age: 20 years) participated in food tasks.

ALE maps

Money

Tasks involving money rewards show concordance in an extensive set of areas (Table 4; Fig. 3). The largest concordant cluster is found to peak in the right caudate head; this cluster extends to the left hemisphere and includes peaks of concordance in the left caudate head, brainstem and bilateral insula. The cluster with the highest likelihood of being detected has a peak on the left anterior cingulate (BA 32); this cluster

Table 2 Characteristics of the erotic studies included in the meta-analyses

Article	n	Age	Foci	Handedness	TR (sec)	Field strength (T)	Task	Contrast
Asensio et al. (2010)	26 (26 males)	28.4 ± 6.3 years	15	right	3	1.5	Letter Discrimination & Passive Viewing	Erotic > neutral pictures
Barrós-Loscertales et al. (2010)	45 (45 males)	21.8 years	19	n/a	3	1.5	Letter Discrimination & Passive Viewing	Erotic > neutral stimuli
Beauregard et al. (2001)	10 (10 males)	23.5 years	9	n/a	3	1.5	Passive Viewing	Erotic > neutral films
Borg et al. (2014)	21 (0 males)	23.0 ± 1.9 years	16	18 right, 3 left	2	3	Passive Viewing	Erotic > neutral pictures
Borg et al. (2014)	21 (0 males)	22.0 ± 2.1 years	12	19 right, 2 left	2	3	Passive Viewing	Erotic > neutral pictures
Brunetti et al. (2008)	18 (18 males)	24.9 years	26	n/a	4.08	1.5	Passive Viewing	Erotic > sports films
Bühler et al. (2008)	10 (10 males)	32.0 ± 5.0 years	14	right	1.8	1.5	Passive Viewing	Erotic > neutral images
Costumero et al. (2013)	45 (45 males)	24.1 ± 3.7 years	23	n/a	2	1.5	Passive Viewing (cued)	Erotic > neutral pictures
Bianchi-Demicheli et al. (2011)	15 (0 males)	30.4 ± 7.1 years	12	right	2.2	3	Passive Viewing	Erotic > non-erotic pictures
Edmiston et al. (2013)	16 (6 males)	39.4 ± 7.6 years	14	n/a	2	3	Passive Viewing	Erotic > neutral pictures
Ferretti et al. (2005)	10 (10 males)	21–25 years	28	n/a	4.08	1.5	Passive Viewing	Erotic > sports films
Graf et al. (2013)	18 (18 males)	25.4 ± 2.9 years	33	n/a	1.5	3	Passive Viewing	Erotic > non- erotic pictures
Hamann et al. (2004)	28 (14 males)	Males: 25.9 years; Females: 25.0 years	10	n/a	4.08	1.5	Passive Viewing	Couples > neutral, non-sexual stimuli
Hu et al. (2008)	10 (10 males)	27.9 ± 3 years	32	n/a	3	1.5	Passive Viewing	Male heterosexuals: heterosexual couple films > baseline
Hu et al. (2011)	14 (14 males)	18–35 years	18	right	3	1.5	Passive Viewing	Heterosexual: erotic > non-erotic stimuli
Kagerer et al. (2011)	21 (21 males)	28.0 ± 4.5 years	10	right	n/a	1.5	Passive Viewing	Most sexually arousing erotic > neutral pictures
Karama et al. (2002)	20 (20 males)	25.0 ± 4 years	18	right	8	1.5	Passive Viewing	Males: erotic > neutral films
Kim et al. (2006)	10 (10 males)	52.0 years	13	right	6	1.5	Passive Viewing	Sexually explicit > emotionally neutral films
Klucken et al. (2013)	100 (49 males)	25.3 ± 4.7 years	11	right	2.5	1.5	Conditioning & Passive Viewing	Erotic pictures > control
Moulier et al. (2006)	10	21.7 years	24	right	5	1.5	Passive Viewing	Sexual arousing > neutral photos
Mouras et al. (2008)	8	18–60 years	22	right	5	1.5	Passive Viewing	Erotic > non-sexual films
Oei et al. (2014)	37 (37 males)	21.5 ± 2.9 years	10	n/a	2.2	3	Backward Masking Task	Erotic pictures > neutral
Paul et al. (2008)	12 (12 males)	33.4 ± 7.2 years	15	n/a	3.5	1.5	Passive Viewing	Heterosexual participants: erotic > neutral films
Ponseti et al. (2006)	53 (27 males)	22.7–27.2 years	13	n/a	3.1	1.5	Passive Viewing	Erotic > non-erotic pictures
Prevost et al. (2010)	16 (16 males)	23.1 ± 18 years	14	right	1.98	3	Delay/ Effort Discounting Task	Reward > effort
Sabatinelli et al. (2007)	22 (11 males)	n/a	12	n/a	3	3	Passive Viewing	Pleasant (erotic) > neutral pictures
Safron et al. (2007)	22 (22 males)	20–26 years	15	right	2.5	3	Passive Viewing	Preferred erotic > sports pictures
Schiffer et al. (2008)	12 (12 males)	36.1 ± 7.5 years	42	11 right, 1 left	3.5	1.5	Passive Viewing	Erotic pictures > neutral pictures
Seo et al. (2010)	21 (21 males)	31.8 ± 8.5 years	2	n/a	2.4	3	Passive Viewing	Erotic pictures > happy faces

Table 2 (continued)

Article	n	Age	Foci	Handedness	TR (sec)	Field strength (T)	Task	Contrast
Sundaram et al. (2010)	14 (14 males)	25 years	19	n/a	3	3	Passive Viewing	Erotic films > rest period
Sylva et al. (2013)	46 (24 males)	22.1 ± 3.1 years	9	right	2.5	3	Passive Viewing	Erotic pictures > baseline
Walter et al. (2008)	21 (11 males)	25.7 years	15	n/a	2	1.5	Passive Viewing	Erotic body photos > non-body photos
Wehrum et al. (2013)	100 (50 males)	25.4 ± 4.8 years	9	right	n/a	1.5	Conditioning, Attention & Passive Viewing	Erotic pictures > neutral pictures
Wehrum-Osinsky et al. (2014)	56 (32 males)	25.9 ± 5.4 years	16	right	2.5	1.5	Conditioning, Attention & Passive Viewing	Erotic pictures > neutral pictures

includes the left medial frontal gyrus BA 10. Laterality indices show that monetary rewards activate all the basal ganglia nuclei bilaterally with the exception of the lateral globus pallidus (LI = 0.23; Fig. 4). Importantly, monetary rewards show concordance extending to the region of interest defined as the nucleus accumbens (LI = −0.02). Compared to food, money rewards show significantly more concordance in the right putamen, left subcallosal gyrus, and left anterior cingulate (BA 32; Table 4). Compared to erotic, money rewards show significantly more concordance in the left medial frontal gyrus (BA 10) and bilateral putamen.

Erotic

The largest concordant cluster for erotic stimuli, which includes the bilateral caudate head and amygdala (Table 4; Fig. 3), has a peak in the left thalamus. The areas with the highest likelihood of being detected are found in the occipito/temporal regions in BA 37. Laterality indices show that erotic rewards elicit activity in all nuclei with the exception of the nucleus accumbens; right dominance is observed in the caudate body (LI = 0.44) and caudate head (LI = 0.21), left dominance is observed in the lateral globus pallidus (LI = −0.45), and putamen (LI = −0.21), whereas the medial globus pallidus (LI = −0.20) was bilateral (Fig. 4). Compared to food, erotic rewards show increased concordance in a set of brain regions that include the left hypothalamus, right cerebellum, bilateral parietal, and frontal cortices (Table 4). Compared to money, erotic rewards show increased concordance in a set of brain areas that include the amygdala, cerebellum, fusiform gyrus, and anterior cingulate (Table 4).

Food

The largest cluster to show concordance for food stimuli is also the one with the highest likelihood of being detected, with peaks over the right insula and bilateral putamen, claustrum, thalamus, and caudate head (Table 4; Fig. 3). Laterality indices show that with the exception of nucleus accumbens, food elicits concordant activity in all basal ganglia nuclei dominant in the left hemisphere: caudate head (LI = −0.53), caudate body (LI = −0.82), putamen (LI = −0.59), lateral globus pallidus (LI = −0.66), and medial globus pallidus (LI = −0.53; Fig. 4). Compared to money, food rewards show increased concordance in areas such as the claustrum, insula and thalamus (Table 4). Similarly, compared to erotic, food rewards show increased concordance in areas such as the claustrum, insula, and putamen.

Conjunction analyses

Table 4 shows results related to conjunction analyses. Results show that both food and money reward show significant

Table 3 Characteristics of the food studies included in the meta-analyses

Article	n	Age	Foci	Handedness	TR (sec)	Field strength (T)	Task	Contrast
Berns et al. (2001)	25	18–43 years	1	n/a	2	1.5	Passive Delivery	Juice > water
de Araujo et al. (2003)	11 (6 males)	n/a	8	right	2	3	Passive Delivery	Sucrose > tasteless solution
Demos et al. (2011)	109 (0 males)	19.0 years	3	n/a	2.5	3	Passive Delivery	Milkshake > water
Eldeghaidy et al. (2011)	18 (10 males)	31.0 ± 10.0 years	29	right	2.6	3	Passive Delivery	Fat > water
Felsted et al. (2010)	40	n/a	13	right	2.53	3	Passive Delivery	Milkshake > tasteless solution
Filbey et al. (2012)	26 (12 males)	32.9 ± 11.0 years	6	right	2	3	Passive Delivery	Positive correlation between sugar content of high-calorie taste
Francis et al. (1999)	6	n/a	8	n/a	2	3	Passive Delivery	Glucose > tasteless artificial saliva
Frank et al. (2012)	23 (0 males)	24.8 years	37	n/a	2.1	3	Classical Conditioning Task	Receiving reward stimulus unexpectedly > artificial saliva
Galvan et al. (2013)	15 (7 males)	28.5 years	17	right	2	3	Passive Delivery	Appetitive liquid > water
Gearhardt et al. (2011)	48 (0 males)	20.8 ± 1.31 years	1	n/a	2	3	Passive Delivery	Milkshake > artificial saliva
Grabenhorst et al. (2010a)	14 (9 males)	24.0 years	6	n/a	2	3	Passive Delivery	Milkshake > tasteless control/rinse solution
Grabenhorst et al. (2010b)	12 (6 males)	24.0 years	10	n/a	2	3	Passive Delivery	Vanilla and strawberry > tasteless solution
Green et al. (2012)	12	24.0 ± 3.3 years	39	n/a	2	3	Passive Delivery	Diet soda drinkers: saccharin > water
Griffioen-Roose et al. (2013)	18 (15 males)	21.0 ± 2.0 years	22	n/a	2.14	3	Classical Conditioning Task	Soft drinks > baseline
Haase et al. (2009)	18 (9 males)	20.7 ± 1.0 years	37	n/a	2	3	Passive Delivery	Sucrose > water
Haase et al. (2011)	9 (9 males)	20.4 years	14	n/a	2	3	Passive Delivery	Males: sucrose > water
Horder et al. (2010)	22 (7 males)	21.4 ± 1.8 years	7	n/a	2	3	Passive Delivery	Strawberry > tasteless solution
Jacobson et al. (2010)	19 (10 males)	23.9 years	15	n/a	2	3	Passive Delivery	Sucrose > water
Kerr et al. (2015)	18 (8 males)	31.0 ± 8 years	3	right	2.5	3	Passive Delivery	Positive correlation with food reward receipt and impulsivity
Kringelbach et al. (2003)	9 (9 males)	28.5 years	5	n/a	2	3	Passive Delivery	Liquid food > tasteless solution
Luo et al. (2015)	24 (10 males)	21.6 ± 2.0 years	16	right	2	3	Passive Delivery	Drink > no drink delivery
McCabe et al. (2007)	12 (6 males)	n/a	5	n/a	2	3	Passive Delivery	MSG and vegetable odor > tasteless solution
McCabe et al. (2011)	15 (7 males)	22.0 ± 2.2 years	9	n/a	2	3	Passive Delivery	Chocolate > tasteless solution
McClure et al. (2004)	33	28.0 ± 7.6 years	1	n/a	2	3	Classical Conditioning Task	Positive correlation with preference for soda drinks
Metereau et al. (2013)	20 (10 males)	24.4 years	18	right	2.5	1.5	Classical Conditioning Task	Positive correlation with apple juice and saltwater
Ng et al. (2011)	34 (0 males)	20.1 ± 1.4 years	2	n/a	2	3	Passive Delivery	High-fat chocolate milkshake > tasteless solution
Nolan et al. (2013)	20 (10 males)	27.0 ± 6.2 years	3	Edinburgh Handedness Inventory score ranging: 55–100	2	3	Passive Delivery	Milkshake > tasteless solution

Table 3 (continued)

Article	n	Age	Foci	Handedness	TR (sec)	Field strength (T)	Task	Contrast
O'Doherty et al. (2001)	7	n/a	14	n/a	2	3	Passive Delivery	Glucose > saltwater
O'Doherty et al. (2002)	8 (5 males)	24.5 years	2	n/a	4.1	2	Classical Conditioning Task	Glucose > tasteless solution
Plassmann et al. (2008)	20 (11 males)	24.5 years	10	right	2	3	Passive Delivery	Wine > tasteless drink
Rolls et al. (2007)	16 (0 males)	n/a	6	n/a	2	3	Passive Delivery	Chocolate > tasteless solution
Rudenga et al. (2013)	30 (18 males)	18–45 years	11	right	2	3	Passive Delivery	Sucrose solution > tasteless solution
Rudenga et al. (2012)	14 (0 males)	27.8 ± 7.7 years	5	11 right	2	3	Passive Delivery	Milkshake > tasteless solution
Seubert et al. (2015)	32 (16 males)	27.0 ± 4.4 years	8	n/a	2.5	3	Passive Delivery	Tastant > baseline
Small et al. (2003)	9 (3 males)	24.0 years	13	right	2.1	1.5	Passive Delivery	Pleasant > tasteless solutions
Small et al. (2008)	12 (5 males)	25.0 years	9	right	2.1	3	Passive Delivery	Drinks > tasteless solution
Smeets et al. (2011)	10 (10 males)	22.4 ± 2.0 years	11	right	3.4	3	Passive Delivery	Food consumption > pre-consumption
Spetter et al. (2010)	15 (15 males)	23.3 ± 1.7 years	9	right	1.6	3	Passive Delivery	Positive correlation with intensity and concentration of taste
Spetter et al. (2012)	15 (15 males)	27.3 ± 1.9 years	16	right	9	3	Passive Delivery	Taste activation > water
Sun et al. (2014)	32 (14 males)	25.5 ± 5.7 years	11	right	2	3	Passive Delivery	Milkshake > tasteless solution
Sweet et al. (2012)	49	n/a	9	right	2.5	3	Passive Delivery	All participants: food stimulation > baseline
Szalay et al. (2012)	24 (6 males)	n/a	16	right	2.5	3	Passive Delivery	Vanilla > water
Takemura et al. (2011)	23 (8 males)	24.0 ± 4.8 years	4	right	2.1	1.5	Classical Conditioning Task	Juice > artificial saliva
Thomas et al. (2015)	16 (8 males)	21.7 ± 0.9 years	7	right	2	3	Passive Delivery	Increased activation when satiated to food delivery
Uher et al. (2006)	8 (8 males)	29.4 ± 7.8 years	3	right	3	1.5	Passive Delivery	Males: chocolate > tasteless solution
Veldhuizen et al. (2011)	16 (0 males)	25.1 ± 6.4 years	21	right	2	3	Passive Delivery	Sweet > tasteless solution

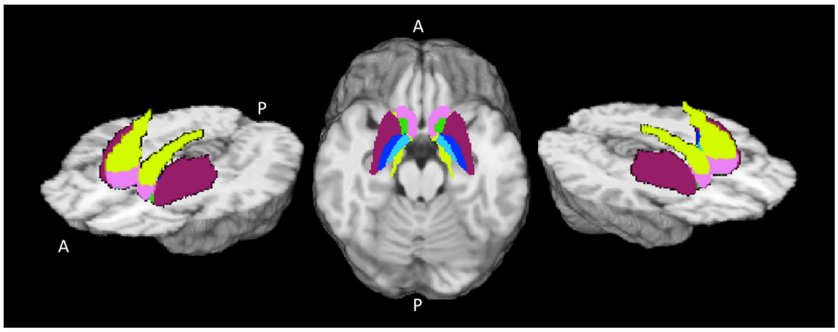

Fig. 2 Basal ganglia nuclei. Regions of interest defined using the TT Daemon template, containing the voxels defined in the San Antonio Talairach Daemon for the nucleus accumbens (green), caudate head (pink), caudate body (yellow), putamen (purple), blue (lateral globus pallidus), and light blue (medial globus pallidus). The caudate tail is not depicted

concordance in bilateral clusters in the putamen and insula, whereas erotic and money rewards show concordance in large clusters in the right caudate head and right anterior cingulate. Our primary reward types, erotic and food rewards, show overlap in the left lateral globus pallidus and right amygdala.

Discussion

We reported concordant data from fMRI studies that examine brain responses to money, erotic, and food reward outcome. Whole-brain responses show common and distinct cortical and sub-cortical regions of activity as a function of our reward types of interest. For instance, monetary rewards elicited extensive activity in the cingulate cortex and left medial frontal gyrus (BA 10). Erotic stimuli elicited extensive activity in the fusiform gyri, amygdala, and inferior frontal gyri. Food stimuli elicited extensive activity in the insula and claustrum. Collectively, our primary and secondary rewards show concordance in basal ganglia nuclei, the main focus of this investigation. All reward types showed concordant activity in the caudate head, caudate body, putamen and medial and lateral globus pallidus; however, distinct patterns were observed in terms of hemispheric dominance. Here, we will highlight the implications of basal ganglia and whole-brain responses as a function of reward and propose a model of reward processing based on stereotaxic coordinates of concordant regions from our meta-analyses.

Regions of interest: basal ganglia nuclei

The basal ganglia are a set of sub-cortical gray matter nuclei, recognized for their critical role in reward processes (Bellebaum et al. 2008; Cohen et al. 2011; Sesack and Grace 2010). Its basic components include the striatum and globus pallidus (Martin 2003), which can be subdivided into seven nuclei: nucleus accumbens, caudate head, caudate body, caudate tail, putamen, medial globus pallidus and lateral globus pallidus. The current results provide novel insight into the specific role of the basal ganglia nuclei to reward processing.

All reward types show concordant clusters with peaks on the caudate head and lateral globus pallidus. Clusters with peaks on the caudate body are observed for erotic and food rewards, whereas clusters with peaks on the putamen are concordant for monetary and food rewards. A cluster with a peak in the medial globus pallidus was only observed for erotic rewards. No concordance was observed for the caudate tail. We note that although peak concordant coordinates are found in different nuclei, in most cases, the clusters are large and extend to adjacent structures. For instance, although peak concordance was not observed as a peak in the nucleus accumbens, we find that only monetary rewards have suprathreshold voxels in the nucleus accumbens.

Traditionally the basal ganglia were discussed in terms of their role in motor actions, originally limited to animal and lesion studies (Haber 2003). fMRI data from healthy adult humans show that the basal ganglia are implicated in all types of body motion, cognitive tasks involving working memory and decision making, as well as emotions and reward processes (Arsalidou et al. 2013). Our current data are consistent with past findings in that reward processes engage all of the basal ganglia nuclei; however previous work (Arsalidou et al. 2013) had not distinguished between different reward types, as done here. A connectivity meta-analysis examining the right and left caudate in healthy humans shows connecting clusters in the middle and inferior frontal gyri, anterior and posterior cingulate gyri, as well as the insula and thalamus (Robinson et al. 2012). Interestingly, hemisphere specific clusters show that the left caudate has more extensive connections with areas such as the red nucleus and the fusiform gyrus (Robinson et al. 2012). Connectivity results appear consistent with our coordinate-based meta-analyses (see the discussion of whole-brain results below), suggesting that there is a relation among these regions; however, the nature of these relations remains unclear. Our data cannot speak to the relation among brain areas, and although functional

Table 4 Concordant structures during monetary, food and erotic reward processing

Money						
Cluster #	Volume mm^3	x	y	z	ALE Value	Brain region
1	28,800	10	8	-2	0.16207	Right Caudate Head
		-10	8	0	0.14202	Left Caudate Head
		6	−16	4	0.04490	Right Thalamus Medial Dorsal Nucleus
		−2	−18	−12	0.04378	Left Red Nucleus
		24	4	8	0.04032	Right Putamen
		−8	−14	−8	0.03952	Left Substania Nigra
		−30	18	8	0.03693	Left Insula BA 13
		32	18	6	0.03526	Right Insula BA 13
		24	−8	2	0.02877	Right Lateral Globus Pallidus
		−24	0	12	0.02781	Left Putamen
		2	−6	10	0.02730	Right Thalamus
		26	−2	−16	0.02469	Right Amygdala
2	5432	−4	44	0	0.05910	Left Anterior Cingulate
		−2	38	16	0.04173	Left Anterior Cingulate BA 32
		−2	50	8	0.04003	Left Medial Frontal Gyrus BA 10
3	2504	−4	−32	28	0.04079	Left Cingulate Gyrus BA 23
		−4	−50	22	0.03480	Left Posterior Cingulate BA 23
4	880	−24	−92	−6	0.03301	Left Lingual Gyrus BA 18
		−24	−92	−10	0.03192	Left Fusiform Gyrus BA 18
Food						
Cluster #	Volume mm^3	x	y	z	ALE Value	Brain region
1	16,696	36	−8	12	0.04739	Right Insula BA 13
		30	14	12	0.04109	Right Insula BA 13
		24	−2	−8	0.04061	Right Putamen
		30	18	6	0.03903	Right Claustrum
		38	6	−4	0.03129	Right Insula BA 13
		58	−6	24	0.02890	Right Precentral Gyrus BA 4
		10	10	2	0.02492	Right Caudate Head
		44	10	4	0.02026	Right Insula BA 13
		36	18	−8	0.01993	Right Inferior Frontal Gyrus BA 47
2	9152	−34	12	12	0.04255	Left Insula BA 13
		−36	−8	10	0.03255	Left Claustrum
		−36	4	−4	0.03174	Left Claustrum
		−52	−16	18	0.02520	Left Postcentral Gyrus BA 43
		−38	−4	0	0.02423	Left Insula BA 13
3	4696	−16	2	4	0.03537	Left Putamen
		−22	−4	−8	0.02905	Left Lateral Globus Pallidus
		−12	8	0	0.02885	Left Lateral Globus Pallidus
		−16	4	16	0.02448	Left Caudate Body
4	1336	12	−16	4	0.02827	Right Thalamus
5	1296	−10	−20	4	0.02555	Left Thalamus Mammillary Body
		−8	−14	10	0.02355	Left Thalamus Medial Dorsal Nucleus
Erotic						
Cluster #	Volume mm^3	x	y	z	ALE Value	Brain region
1	16,168	−2	−10	8	0.04627	Left Thalamus Medial Dorsal Nucleus
		6	10	0	0.04524	Right Caudate Head
		−20	−2	−10	0.04200	Left Amygdala
		16	−4	−8	0.04198	Right Medial Globus Pallidus

Table 4 (continued)

		20	−2	−12	0.04151	Right Amygdala
		−10	4	2	0.03676	Left Lateral Globus Pallidus
		−4	8	0	0.03631	Left Caudate Head
		−2	−6	−6	0.03546	Left Hypothalamus
		4	−24	6	0.02375	Right Thalamus Pulvinar
		8	4	10	0.02270	Right Caudate Body
2	4264	42	−62	−8	0.04589	Right Fusiform Gyrus BA 37
		42	−50	−16	0.02823	Right Fusiform Gyrus BA 37
		40	−46	−14	0.02770	Right Fusiform Gyrus BA 37
3	2320	0	34	14	0.04170	Left Anterior Cingulate BA 24
		−6	42	8	0.03020	Left Anterior Cingulate BA 32
		2	50	14	0.01834	Right Medial Frontal Gyrus BA 10
4	1968	−46	−64	−8	0.04276	Left Middle Occipital Gyrus BA 37
5	1880	26	−54	50	0.03618	Right Precuneus BA 7
6	1720	44	2	28	0.04440	Right Inferior Frontal Gyrus BA 9
7	1656	−32	−52	46	0.03461	Left Superior Parietal Lobule BA 7
		−22	−66	42	0.02343	Left Superior Parietal Lobule BA 7
8	1336	−26	12	−10	0.03274	Left Inferior Frontal Gyrus BA 13
		−36	16	−4	0.01993	Left Inferior Frontal Gyrus BA 47
9	1000	−46	2	28	0.03623	Left Precentral Gyrus BA 6
Conjunction: Money_AND_Food						
Cluster #	Volume mm^3	x	y	z	ALE Value	Brain region
1	3032	−16	2	4	0.03537	Left Putamen
		−12	8	0	0.02885	Left Lateral Globus Pallidus
		−22	−4	−8	0.02760	Left Lateral Globus Pallidus
2	2272	22	0	−6	0.03345	Right Putamen
		10	10	2	0.02492	Right Caudate Head
3	952	32	18	6	0.03526	Right Insula BA 13
		28	6	8	0.01971	Right Putamen
		28	8	4	0.01905	Right Putamen
4	552	−32	18	10	0.03249	Left Insula BA 13
5	400	10	−16	4	0.02668	Right Thalamus
6	56	26	10	10	0.01874	Right Putamen
7	18	40	8	4	0.01726	Right Insula BA 13
8	8	30	4	2	0.01706	Right Putamen
Conjunction: Money_AND_Erotic						
Cluster #	Volume mm^3	x	y	z	ALE Value	Brain region
1	7856	6	10	0	0.04524	Right Caudate Head
		−20	−2	−8	0.04012	Left Lateral Globus Pallidus
		−10	4	2	0.03676	Left Lateral Globus Pallidus
		−4	8	0	0.03631	Left Caudate Head
		16	−2	−6	0.03629	Right Medial Globus Pallidus
		24	−2	−16	0.02397	Right Amygdala
		−4	−2	6	0.02388	Left Thalamus Anterior Nucleus
		−8	−6	−6	0.02279	Left Hypothalamus
		8	4	10	0.02270	Right Caudate Body
2	1080	−2	36	14	0.03504	Left Anterior Cingulate BA 32
		−4	44	8	0.02706	Left Anterior Cingulate BA 32
3	632	4	−14	8	0.02869	Right Thalamus Medial Dorsal Nucleus
		2	−8	10	0.02673	Right Thalamus
4	8	−6	−10	−6	0.01675	Left Subthalamic Nucleus
5	8	6	−4	4	0.01661	Right Thalamus
6	8	−8	−4	6	0.01734	Left Thalamus Ventral Anterior Nucleus
Conjunction: Erotic_AND_Food						
Cluster #	Volume mm^3	x	y	z	ALE Value	Brain region
1	1800	−22	−4	−8	0.02905	Left Lateral Globus Pallidus
		−12	6	2	0.02806	Left Lateral Globus Pallidus
2	1064	22	−2	−10	0.03393	Right Amygdala
3	736	10	10	2	0.02492	Right Caudate Head
4	216	−6	−14	8	0.02232	Left Thalamus Medial Dorsal Nucleus
5	40	6	−20	6	0.01701	Right Thalamus Medial Dorsal Nucleus
6	32	−28	16	−4	0.01567	Left Insula BA 13
7	8	6	−16	6	0.01654	Right Thalamus Medial Dorsal Nucleus

Table 4 (continued)

Contrast: Money > Food						
Cluster #	Volume mm^3	x	y	z	*P* value	Brain region
1	1800	12	8.7	−2.7	0.00010	Right Lateral Globus Pallidus
		16	10	−1	0.00020	Right Putamen
		20	10	2	0.00040	Right Putamen
2	1224	−10	6	−10	0.00030	Left Sub-lobar Gray Matter
		−14	7	−10	0.00040	Left Putamen
3	552	−8	42	−4	0.00110	Left Anterior Cingulate BA 32
		−4	44	−6	0.00130	Left Anterior Cingulate BA 32
4	496	4	38	20	0.00140	Right Anterior Cingulate BA 32
		−2	36	22	0.00240	Left Anterior Cingulate BA 32
		0	34	18	0.00290	Left Anterior Cingulate BA 32
		−6	34	18	0.00400	Left Anterior Cingulate BA 32
5	328	−28	−91	−4	0.00110	Left Inferior Occipital Gyrus BA 18
Contrast: Money > Erotic						
Cluster #	Volume mm^3	x	y	z	P value	Brain region
1	800	0	50	−6	0.00020	Left Medial Frontal Gyrus BA 10
		−4	50	−6	0.00030	Left Medial Frontal Gyrus BA 10
2	736	16	6	−4	0.00070	Right Putamen
		24	2	2	0.00170	Right Putamen
		26	−8	6	0.00620	Right Putamen
3	576	−20	11	1	0.00020	Left Putamen
Contrast: Food > Money						
Cluster #	Volume mm^3	x	y	z	P value	Brain region
1	8720	48.2	−6.5	17.3	0.00010	Right Precentral Gyrus BA 6
		32.5	−3.3	11.8	0.00010	Right Claustrum
		28	8	−10	0.00040	Right Subcallosal Gyrus BA 34
		33.3	4.7	11.3	0.00050	Right Claustrum
		30	12	8	0.00130	Right Claustrum
		26	−5	−10	0.00160	Right Amygdala
2	6408	−39.9	−3.4	10.3	0.00620	Left Insula BA 13
		−37.2	−10.6	9.7	0.00020	Left Insula BA 13
		−40	−16	14	0.00020	Left Insula BA 13
		−54	−10	15	0.00120	Left Postcentral Gyrus BA 43
		−32	16	2	0.00300	Left Claustrum
3	368	14	−18	3	0.00190	Right Thalamus
		−8	−24	6	0.00210	Left Thalamus Pulvinar
4	360	−6	−16	10	0.00310	Left Thalamus Medial Dorsal Nucleus
Contrast: Food > Erotic						
Cluster #	Volume mm^3	x	y	z	P value	Brain region
1	3856	36.6	−10.9	15	0.00010	Right Insula BA 13
		55.4	−7	19.3	0.00020	Right Postcentral Gyrus BA 43
		58.4	−5.8	26.2	0.00020	Right Precentral Gyrus BA 4
		62	0	20	0.00030	Right Precentral Gyrus BA 6
2	2024	−48	−10	15	0.00060	Left Precentral Gyrus BA 13
		−34	−14	16	0.00070	Left Insula BA 13
		−39	−12	17	0.00110	Left Insula BA 13
		−52	−10	14	0.00100	Left Precentral Gyrus BA 43
		−54	−10	20	0.00110	Left Postcentral Gyrus BA 43
		−30	−10	10	0.00210	Left Putamen
		−48	−18	26	0.00290	Left Postcentral Gyrus BA 2
3	392	−40	12	14	0.00130	Left Insula BA 13
Contrast: Erotic > Food						
Cluster #	Volume mm^3	x	y	z	P value	Brain region
1	5504	−0.7	−1.4	0.2	0.00000	Left Caudate Head
		2	14	−3	0.00010	Right Anterior Cingulate BA 25
		0	9	−2	0.00020	Left Anterior Cingulate BA 25
		−2	10	−6	0.00030	Left Anterior Cingulate BA 25
		14	−6	−8	0.00140	Right Medial Globus Pallidus
		0	−19	10	0.00310	Left Thalamus
		12	0	−10	0.00530	Right Subcallosal Gyrus BA 34
2	4208	43.2	−60.5	−8.6	0.00000	Right Fusiform Gyrus BA 37
3	1704	−45.3	−62.7	−8.9	0.00000	Left Fusiform Gyrus BA 37
		−50.5	−68	−7	0.00020	Left Middle Occipital Gyrus BA 19

Table 4 (continued)

4	1424	−28.8	−52.7	42.5	0.00000	Left Superior Parietal Lobule BA 7
		−24	−62.5	43.5	0.00010	Left Superior Parietal Lobule BA 7
5	1408	29.6	−54.9	55.8	0.00000	Right Superior Parietal Lobule BA 7
6	1384	−9	37	10	0.00020	Left Anterior Cingulate BA 32
		−6	32	10	0.00020	Left Anterior Cingulate BA 24
7	1352	39.4	1.3	31.5	0.00000	Right Precentral Gyrus BA 6
8	576	−45	4	28	0.00150	Left Inferior Frontal Gyrus BA 9
9	512	−26	2	−16	0.00130	Left BA 34
10	368	−32	18	−12	0.00110	Left Inferior Frontal Gyrus BA 47
Contrast: Erotic > Money						
Cluster #	Volume mm^3	x	y	z	P value	Brain region
1	6232	−0.4	−3.9	−4.3	0.00000	Left Hypothalamus
		−5	−17	11	0.00020	Left Thalamus Medial Dorsal Nucleus
		7	−14	−1	0.71420	Right Thalamus
2	4232	42.6	−61.2	−8.5	0.00000	Right Fusiform Gyrus BA 37
3	1856	26.2	−56.7	51.1	0.00000	Right Precuneus BA 7
4	1816	−47.6	−67.7	−4.7	0.00000	Left Middle Occipital Gyrus BA 37
5	1688	42.7	2.7	27	0.00000	Right Precentral Gyrus BA 6
		38.9	0.2	30.9	0.00010	Right Precentral Gyrus BA 6
6	1472	−20.9	−2.3	−17.1	0.00000	Left Amygdala
7	1360	−34	−49.2	46.4	0.00010	Left Inferior Parietal Lobule BA 40
		−32	−52	44	0.00010	Left Inferior Parietal Lobule BA 40
		−25	−65	46	0.00030	Left Superior Parietal Lobule BA 7
8	912	−5	39	10	0.00450	Left Anterior Cingulate BA 32
9	824	−28.8	12.8	−12.7	0.00000	Left Inferior Frontal Gyrus BA 13
10	672	−49.7	−1	29.3	0.00000	Left Precentral Gyrus BA 6

connectivity analyses can identify relations among brain areas, it cannot describe the causal nature of the relation; thus, further research is needed. However, by examining both basal ganglia and whole-brain concordance within and across our reward types, we can speculate how the basal ganglia act as a core contributor in general reward processing in conjunction with other cortical and sub-cortical regions.

Whole-brain: cortical and sub-cortical contributions

Frontal cortex

Processing food stimuli showed concordance in right precentral and inferior frontal gyri. Processing erotic stimuli showed concordance in inferior frontal gyri bilaterally, left precentral gyrus,

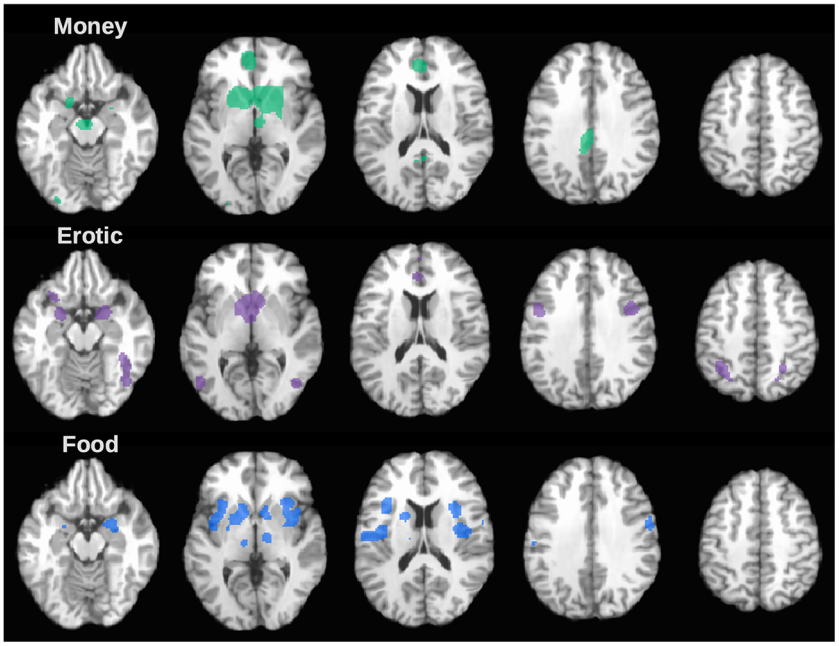

Fig. 3 Axial images depicting significant concordant clusters for money (green), erotic (purple) and food (blue) rewards

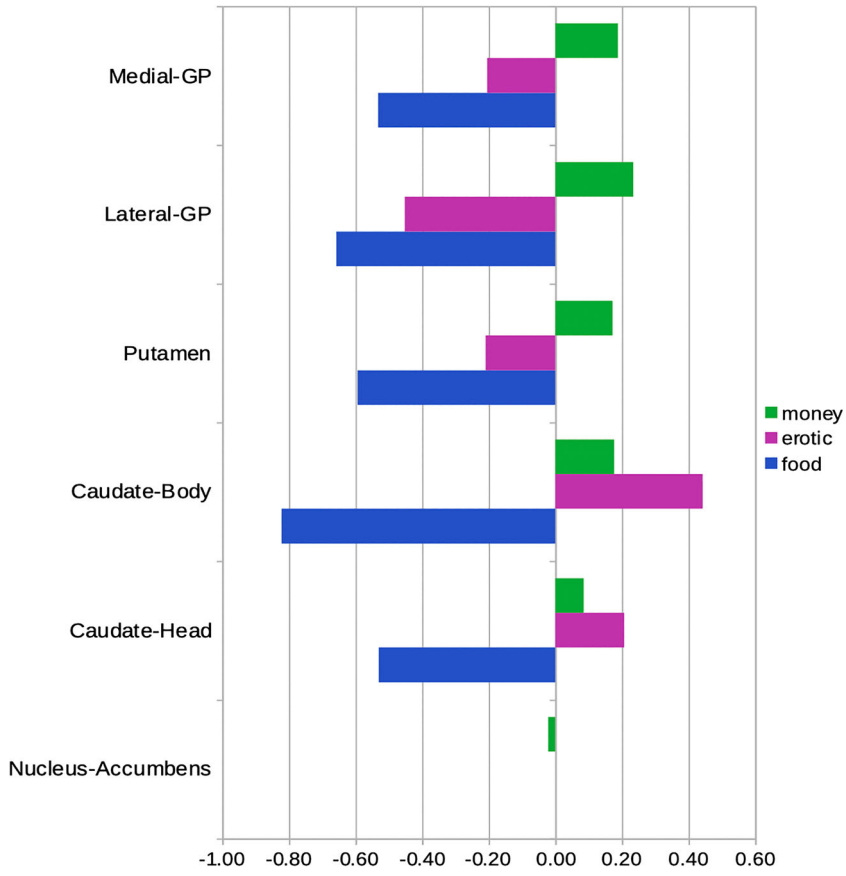

Fig. 4 Laterality indices for basal ganglia structures. Hemisphere dominance was calculated for each region by applying the region of interest masks to the threshold ALE maps. Laterality index (LI = [Right– Left]/ [Left + Right]) of >0.20 was classified as right dominance and < −0.20 left dominance, with values in between considered bilateral. GP = globus pallidus

and right medial frontal gyrus (BA 10). Processing monetary stimuli also activated the medial frontal gyrus (BA10), but in the left hemisphere. Moreover, anterior cingulate is concordant when processing money and erotic stimuli, but not food stimuli.

Precentral gyri have been associated with processes such as motor/action planning (de Lange et al. 2008; Johnson-Frey et al. 2005; Riehle and Requin 1989) and eye movements (Anderson et al. 2012; Grosbras et al. 2005; Petit et al. 1993). According to early work on the mapping of the cortical homunculus, middle parts of the precentral gyrus correspond to hand and eye movements, whereas inferior parts correspond to the mouth, lips and tongue (Penfield and Boldrey 1937). This may be consistent with a mouth-reaction from the sampling of sweet and tasty flavours when participants received food in their mouth. In these studies, the food was provided through a tube so that participants could taste it without really seeing the food.

Inferior frontal gyri have been associated with all sorts of cognitive and affective tasks. Our meta-analyses show inferior frontal gyrus concordance for food in the right hemisphere and erotic stimuli bilaterally. In a model of prefrontal organization, Christoff and colleagues propose that the inferior frontal gyri (BA 45/47) support processing of few externally driven features with low levels of abstraction (Christoff and Gabrieli 2000; Christoff et al. 2009). It is therefore consistent that processing food stimuli may require lower levels of abstraction than stimuli with erotic content.

Indeed, erotic stimuli additionally elicit activity in the right medial frontal gyrus, a region we also find concordant for stimuli involving money in the left hemisphere. Medial frontal gyri (BA 10) activity has been extensively discussed for their role in reward (Gehring and Willoughby 2002; Pochon et al. 2002). However, this region also engages for future-oriented processes (Bar, 2010), higher-level decision making (Rogers et al. 2004; Xue et al. 2009), and is part of the default mode network (Sharaev et al. 2016; Spreng et al. 2008). The model of prefrontal organization proposes the medial frontal cortex is an area of high abstraction that manipulates internally generated information (Christoff and Gabrieli 2000; Christoff et al. 2009). Processing monetary and erotic stimuli may involve internalized thoughts and higher levels of abstraction; however, it is unclear from the model under which circumstances the right or left hemisphere should be implicated. Hemispheric involvement, in this case, may also depend on the level of difficulty of the task. For instance, processing of internally generated information in monetary tasks may require planning and evaluation of action consequences, whereas processing of erotic stimuli may be more automatic. This is consistent with the Right-

Left-Right hypothesis that suggests that tasks that are too easy (i.e., automatic) tend to favor the right hemisphere, whereas tasks that are within the individual's limit of mental-attentional capacity favor the left hemisphere (Arsalidou and Pascual-Leone 2016; Pascual-Leone 1989). The Right-Left-Right model also explains that when the task is above the mental attentional capacity of the individual (i.e., too difficult) the individual will revert to automatic processes to generate a solution; thus favoring the right hemisphere (Arsalidou and Pascual-Leone 2016; Pascual-Leone 1989). Our data appear consistent with this hypothesis; however, future targeted investigations are needed for clarification.

Concordant clusters in the anterior cingulate were observed only for monetary and erotic stimuli. Anterior parts of the cingulate have been associated with executive attention involved in tasks of mental-attention and working memory (Arsalidou et al. 2013; Owen et al. 2005 for meta-analyses). Consequently, it has been suggested that this region plays a coordinating role in multiple attentional systems (Peterson et al. 1999), and multimodal functions (Shackman et al. 2011) of varying task complexity (Torta et al. 2013). It is also suggested that its role could be to convert current affective intentions into cognitive goals (Arsalidou et al. 2013; Arsalidou and Pascual-Leone 2016). We propose that dorsal cingulate regions are involved in externally driven motivated attention for keeping with the goals of the task.

Posterior cortex

Erotic stimuli show the most extensive concordance in middle occipital and fusiform gyri and the superior parietal lobule and precuneus. Concordance associated with food stimuli is observed in the postcentral gyrus (BA 43), whereas monetary rewards engage the left lingual gyrus and the posterior cingulate (BA 23). The posterior cingulate has been discussed for its role in memory, prospection, navigation, theory of mind and the default mode network (Spreng et al. 2008 for meta-analyses). We propose that posterior regions of the cingulate gyri are involved in internally driven motivated attention needed for keeping with the goals of the task. The postcentral gyrus (BA 43) located at the base of the inferior parietal lobule, below the somatosensory cortex, is a primary gustatory area (Iozzo et al. 2012; Veldhuizen et al. 2011; Wang et al. 2004), consistent with the task involved in this reward type. Occipito-temporal and occipito-parietal networks have been associated with processing many forms of visual-spatial stimuli (Kravitz et al. 2011; Vaina 1989). Importantly, however, areas such as the fusiform, lingual, and occipital gyri have been associated in imagining of past and future events (Addis et al. 2009; Botzung et al. 2008). The fusiform gyrus, which is extensively activated in erotic tasks, is also implicated in visual creativity (Pidgeon et al. 2016 for a meta-analysis). This may support the notion that erotic stimuli elicit more visual creativity and imagination compared to monetary and food stimuli.

Sub-cortical and sub-lobar

In addition to extensive concordance in basal ganglia nuclei, all reward types show concordance in the thalamus. The thalamus is known as the gateway to the cerebral cortex, it is located between the midbrain and the cortex (Pinault 2004). It serves as a relay station between cortical and subcortical regions (Nadeau 2008), being implicated in execution of responses (Huettel et al. 2001) and executive-control (Marzinzik et al. 2008). It shows strong connections to midbrain structures such as the substantia nigra (Bianciardi et al. 2016), and affects cortico–thalamo–cortical (Nadeau 2008) and cortico-cortical communications (Sherman and Guillery 2002). We propose that the thalamus, together with other subcortical structures, assign priority values for gateway access and converging information.

Amygdalae, known for their involvement in core affective processes, show concordance for tasks involving erotic stimuli bilaterally. Paradigms involving emotional processing such as anger and happiness (e.g., Arsalidou et al. 2011), trustworthiness (Santos et al. 2016 for meta-analyses), and associative learning (Ehrlich and Josselyn 2016; Likhtik and Paz 2015 for reviews) elicit activity in the amygdalae. Its role in reward processing has also been extensively discussed (Elliott et al. 2004; Liu et al. 2011; Zalla et al. 2000). Congruently, we propose that the amygdalae may assign an affective value to the stimuli that could reflect a potential ontogenetic gain.

The claustrum is concordant only for food stimuli. The claustrum is a strip of cortex that is anatomically and functionally distinct from its neighbours the insula and the basal ganglia (Mathur 2014; Park et al. 2012). The main hypothesis regarding its functionality is that it is a cross-modal integrator needed for forming conscious percepts (Crick and Koch 2005; Goll et al. 2015). Although most food tasks involved passive tasting, some studies asked participants to provide a pleasantness rating. Perhaps the claustrum distinctly activates to food stimuli as participants needed to create precepts of the food they were sampling.

Food stimuli show the most extensive concordance in the insular cortex. The insula is a sub-lobar region that joins the temporal and the frontal lobes. In terms of function, the insulae became known for their role in affective processes (Duerden et al. 2013; Gu et al. 2013 for meta-analyses). Currently, their role has transformed to one that brings together cognition, emotion and interoception (Uddin et al. 2014). This is consistent with the hypothesis that suggests the insulae may be involved in intrinsically motivated behaviors (Arsalidou and Pascual-Leone 2016; Pascual-Leone et al. 2015; Sridharan et al. 2008; Uddin and Menon 2009). Such understanding may be also relevant for tasks containing

reward as the insulae would serve to switch between self-driven motivations and attention to the task at hand; perhaps food stimuli from our data were less captivating compared to tasks involving money and erotic stimuli, thus required more toggling between self-driven motivations and attention.

Substantia nigra and red nucleus are adjacent parts of the midbrain, initially associated motor control functions (Groenewegen 2003; Lehericy et al. 2006). However, recent work also shows their involvement in processes of learning and reward (Matsumoto and Hikosaka 2007; Schultz 2004); knowledge derived mainly from animal models. An elegant human functional connectivity study used region of interest templates derived from high resolution 7-Tesla anatomical images to show connectivity metrics with local and distal brain regions, suggestive of their critical role in defining brain-behavior relations (Bianciardi et al. 2016). Behaviors such as response selection and the delay period related to proactive control elicit activity in the substantia nigra, supporting the hypothesis that this region is involved in higher-order cognitive functions (Yoon et al. 2014). We propose that midbrain regions may engage in processing monetary rewards due to the increased requirements for decision making needed by such tasks.

Models of reward

Given the current knowledge we speculate on the plausible factors that drive variation in basal ganglia contribution to reward processes in healthy humans. Our data show that money, food, and erotic reward processes implicate the basal ganglia in addition to some other common and distinct parts of the brain. For this reason, we conclude by proposing a basal ganglia model that is common across all rewards types as well as models that show interaction of basal ganglia nuclei with cortical and sub-cortical regions (Fig. 5). Converging evidence across our primary and secondary reward types suggest that basal ganglia nuclei such as the caudate, putamen, and globus pallidus compose a common reward processing circuit. These nuclei could be considered as a basic subcortical structure driving reward processes irrespective of the reward outcome type or contextual factors associated with the reward receipt.

Possible models for the three reward types are also proposed (Fig. 5). These models include the thalamus, which may serve as a bridge between subcortical and cortical regions in all types of reward processing. We include the left thalamus in our food and erotic reward processing models, and right thalamus in the money reward processing model. The selection of brain areas and dominant hemispheres were made based on higher ALE scores (Table 4). For instance, the most concordant cortical region for (a) monetary reward is the left anterior cingulate, (b) erotic reward is the right fusiform gyrus, and (c) food reward is the right insula. Notably, there could be many options for brain areas involved in each type of reward process, but here we propose simple models with the same number of nodes, so that they are comparable. The motivation for developing reward models of basal-ganglia interaction with other brain regions using the same number of nodes is to generate evidence-based models for hypotheses testing in future research, using methods such as Dynamic Causal Modeling (DCM: Friston et al. 2003). Specifically, in a

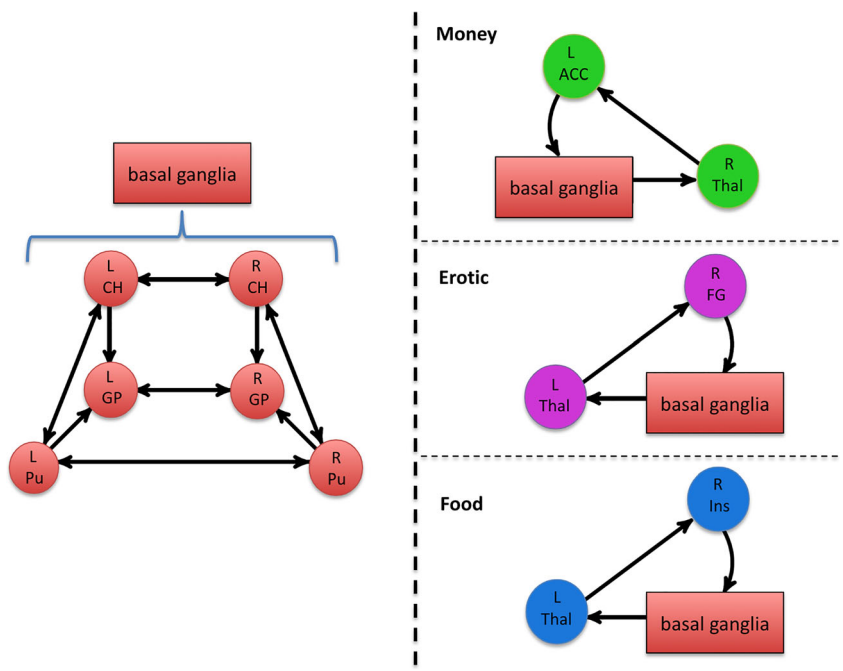

Fig. 5 Proposed connectivity models for the basal ganglia and their involvement in money, erotic and food rewards. Arrows represent uni- and bi-directional connections. L = Left, R = Right, CH = caudate head, GP = globus pallidus, Pu = putamen, Thal = Thalamus, ACC = anterior cingulate cortex, FG = fusiform gyrus, Ins = insula

Bayesian framework, which allows for model inversion and comparison, uni-directional and bi-directional connections can be examined. In order to perform comparisons across our reward models, it is optimal that the models are matched in terms of the number of nodes they contain. Proposed connections indicated by bidirectional and unidirectional arrows (Fig. 5) are derived from seminal studies of anatomy and neurochemistry of cortico-basal ganglia-thalamo-cortical loop (Parent and Hazrati 1995). Putamen and caudate have outgoing connections to the globus pallidus, which in turn has projections with the thalamus (Ikemoto et al. 2015). The thalamus has wide ranging projections to different cortical areas, and the loop is closed by back cortical projections to the striatum (Silkis 2001; Utter and Basso 2008). Critically these projections have not been tested directly in healthy human participants, as previous connectivity models are based on animal and human patient studies.

Limitations

The current study includes limitations common to general meta-analytic methodology. For example, a different number of articles and foci for food and erotic rewards could possibly lead to less statistical power in comparison to monetary rewards, however, all categories had well over the current minimum recommendation of experiments ($n = 17$–20) needed for a meta-analysis (Eickhoff et al. 2016) and supplementary analyses (not shown) yielded comparable results when split-half datasets of monetary reward were analyzed separately. Related to the diverse sample of studies used, fMRI acquisition differences in our selected sample may have also biased the results we found. Given the nature of meta-analytic methodology, we cannot control for all the fMRI acquisition differences such as variability in MRI equipment manufacturer parameters, acquisition field strength, statistical procedures, and thresholds, however, we report for consideration some behavioral and fMRI study parameters for each study in Tables 1, 2 and 3. Furthermore, to test whether differences in a crucial fMRI parameter, repetition time (TR), impacted our results, we conducted the analyses with studies with TR less than 2500 ms and greater than 2500 ms for each reward type when $n > 17$ experiments were available and found the results to be comparable. Lastly, there was large variation in the gender distribution of our final sample for food and erotic reward studies: food reward contained predominantly female participants, whereas studies with erotic rewards had predominantly male participants. It would have been ideal to match our money, food, and erotic reward samples with similar amounts of males and females, or to have reported our results separately for each sex. However, in addition to gender demographics reported in Tables 1, 2 and 3 we did not have a sufficient number of studies that report activation peak coordinates for male and females separately in our money ($n = 0$ male/female only), food ($n = 2$ male only), and erotic ($n = 5$ male only) reward groups.

Conclusion

In this investigation, we analyzed fMRI studies investigating reward processing in healthy adult humans. We identified basal ganglia nuclei and whole-brain contributions to money, food, and erotic rewards, and proposed novel models of reward processing that suggest the role of basal ganglia in driving reward processing within the whole-brain. Based on ALE scores, we found that all types of reward engage the caudate head, putamen and globus pallidus, supporting the idea that basal ganglia play a central role in general reward processing. The current data highlight that hemispheric dominance varies across basal ganglia nuclei as a function of reward type: food rewards favour the left hemisphere; money rewards are mainly bilateral, whereas erotic rewards show a more complex pattern. We also proposed three biologically plausible reward system models of functional integration among basal ganglia, cortical, and subcortical subregions that may motivate future research in the reward functions of the basal ganglia.

Acknowledgements We gratefully acknowledge support from the Russian Science Foundation #17-18-01047 to MA. MS was supported by Skolkovo Biomedical Initiative and Russian Foundation for Basic Research according to the research project № 17-29-02518 (mathematical modeling of brain connectivity).

Compliance with ethical standards

Conflict of interest Authors have no conflict of interest to declare.

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