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The centre of the brain: Topographical model of motor, cognitive, affective, and somatosensory functions of the basal ganglia

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The Centre of the Brain: Topographical Model of Motor, Cognitive, Affective, and Somatosensory Functions of the Basal Ganglia

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Abstract: The basal ganglia have traditionally been viewed as motor processing nuclei; however, functional neuroimaging evidence has implicated these structures in more complex cognitive and affective processes that are fundamental for a range of human activities. Using quantitative meta-analysis methods we assessed the functional subdivisions of basal ganglia nuclei in relation to motor (body and eye movements), cognitive (working-memory and executive), affective (emotion and reward) and somatosensory functions in healthy participants. We document affective processes in the anterior parts of the caudate head with the most overlap within the left hemisphere. Cognitive processes showed the most widespread response, whereas motor processes occupied more central structures. On the basis of these demonstrated functional roles of the basal ganglia, we provide a new comprehensive topographical model of these nuclei and insight into how they are linked to a wide range of behaviors. *Hum Brain Mapp 34:3031–3054, 2013.* © 2012 Wiley Periodicals, Inc.

Key words: caudate; putamen; globus pallidus; functional subdivision; Activation Likelihood Estimate method

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INTRODUCTION

The basal ganglia are a set of deep gray matter nuclei situated in the centre of the brain, at the base of the forebrain. The basic components include the striatum (composed of three subnuclei: the caudate, the putamen, and nucleus accumbens) and the globus pallidus [Martin, 2003]. Knowledge of the functional roles of the basal ganglia has been largely based on patients with motor dysfunction such as Parkinson's disease [Chenery et al., 2008; Dagher and Nagano-Saito, 2007] and Huntington's disease [Bohanna et al., 2008; Paulsen, 2009], which led the field to associate these nuclei primarily with motor functions. However, these subcortical nuclei are also implicated in cognitive disorders, such as attention-deficit/hyperactivity disorder [Aron and Poldrack, 2005; Bush et al., 2005; Knutson and Gibbs, 2007] and obsessive/compulsive disorder [Huyser et al., 2009]. Furthermore, evidence from functional magnetic resonance imaging (fMRI) has suggested more complex roles for the basal ganglia in processing higher cognitive functions, emotion, and somatosensation. Despite the recent surge of fMRI evidence, the processes subserved by the basal ganglia were characterized as mysterious [Mazzoni and Bracewell, 2010] and the most recent topographical model of basal ganglia function was published more than two decades ago [Alexander et al., 1990]. A wealth of functional neuroimaging data can now be analyzed to improve our understanding of these central brain structures. Thus, we compiled and analyzed existing fMRI data, collected from healthy adults, to examine functional subdivisions of the basal ganglia and to provide an updated topographical model of the various functions: motor, cognitive, affective, and somatosensory, within the nuclei of the basal ganglia.

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Basal ganglia involvement in motor behavior is possibly its longest known function and the most thoroughly researched [Mattay and Weinberger, 1999; Ungerleider et al., 2002]. More recent qualitative reviews have attributed cognitive functions to the basal ganglia including reinforcement learning [Bullock et al., 2009], category learning [Nomura and Reber, 2008; Shohamy et al., 2008], sequential decision-making [Cabeza and Nyberg, 2000], working memory training [Dahlin et al., 2009] and learning based on evaluation of outcomes [Frank and Claus, 2006; Grahn et al., 2008]. The nucleus accumbens, part of the ventral striatum, has been implicated in reward-related processes [Assadi, et al., 2009; Delgado 2007], such as anticipation of monetary gains [Knutson and Bossaerts, 2007; Knutson and Greer, 2008; Knutson and Peterson, 2005].

Functional subdivisions of the basal ganglia have been proposed based on qualitative evidence, suggesting that motor selection, preparation and execution processes are subserved by the rostrocaudal parts of the basal ganglia (i.e., largely the putamen), eye-movements implicate the caudate, whereas reward-processes involve the ventral aspects of the basal ganglia [Lehericy and Gerardin, 2002]. Alexander et al., [1990] proposed the most comprehensive functional model of the basal ganglia to date, thus we frequently refer to and make contrasts with this previous work. Primarily based on animal and pathology studies they illustrated five systems of cortical areas that receive output from the basal ganglia [Alexander et al., 1990]. These five cortical categories were motor, oculomotor, cognitive dorsolateral (related to the prefrontal cortex Brodmann areas 9 and 10), cognitive lateral-orbitofrontal (related to the prefrontal cortex Brodmann area 10) and limbic. While this work provided insight into the functional subdivisions of the basal ganglia, more recent neuroimaging studies have produced a wealth of evidence on how these nuclei are involved in cognitive and physiological processes such as reward and somatosensory processing in healthy humans. Therefore, an updated function-based model of the basal ganglia based on quantitative human brain imaging data is warranted.

We built on the previously proposed categories [Alexander et al., 1990] to define motor, cognitive, affective, and somatosensory functions into seven categories: motor (1) body movements and (2) eye movements; cognitive (3) working-memory, such as storing and manipulating information and (4) executive functioning that requires the creation of an executive scheme, such as planning; affective (5) emotion—eliciting and perceiving emotions and (6) reward—receiving positive/negative feedback and monetary outcomes; and (7) sensory—processes that involve somatosensation, primarily the perception of noxious stimuli. These functions are not necessarily processed by distinct locations in separate nuclei; therefore, an overlap of some categories was expected.

To create a functional atlas of the basal ganglia we used a data-driven, coordinate-based meta-analytic technique (Activation Likelihood Estimate, ALE) [Laird et al., 2005; Turkeltaub et al., 2002]. This method calculates the probability that a given voxel in the brain is activated consistently across studies. First, 3D-probabilistic maps of each of the categories were created to quantify the spatial extent and localization of motor-, cognitive-, affective-, somatosensory-evoked activation in specific nuclei in the basal ganglia. Second, laterality indices were calculated to identify hemispheric asymmetries related to each nucleus and each function. Specifically, we examined functional distinctions in the basal ganglia elicited by body movements and eye movements. We also looked at distinctions between different cognitive and affective functions as well as somatosensory processes. We provide normative fMRI atlases for these processes in standard stereotaxic space as well as topographical models that characterize basal ganglia functions in terms of significant peak ALE values and lateralization.

METHODS

Literature Search and Article Selection

The literature was searched using the standard search engine of Web of Science (http://www.isiknowledge.com). In October 2010, we looked for fMRI articles that mentioned the basal ganglia in the whole document (e.g., abstract, main text, and references) by using keywords such as (fMRI and basal ganglia, striatum, caudate, putamen, lentiform/lenticular nucleus, globus pallidus, nucleus accumbens). To maintain interpretability based on imaging method we only selected fMRI studies and did not include positron emission tomography (PET) studies in the search criteria. The inclusion of data obtained from one functional neuroimaging technique has a number of advantages when performing meta-analyses. Namely, it reduces variability in the data and this is an important consideration given that the temporal and spatial resolution of PET is poorer in comparison to fMRI. Articles were also restricted to include human participants and to be in English. This search, which yielded a total of 1,848 studies, was subjected to two successive criteria to identify articles that used fMRI and reported coordinates from the basal ganglia; 699 were neither fMRI studies nor reported coordinates in the basal ganglia, and were excluded. Of these 699 articles, 147 were reviews and 16 were case studies. The remaining 1,149 studies were incorporated in a full text review. To preserve data interpretability, we only considered studies that included healthy independent adult samples (ages: 17/18–65) with within-group results that clearly stated using whole-brain random-effects analyses. We only considered studies that reported positive activations (not deactivations) related to the basal ganglia using either the Talairach or Montreal Neurological Institute (MNI) coordinate systems. The data from 204 studies passed these criteria and were included in the analyses (Table I).

TABLE I. Characteristics of sources included in the meta-analyses

	Participants						
Author-year	*N*	F	Age (M ± SD)	Task	Contrast	Category	Foci
Abutalebi et al., 2008	12	10	25.4 ± 4.3	Bilingual naming task	native 1st language: language selection context > simple naming context	WM	3
Akine et al., 2007	9	2	32.6 ± 7.2	False recognition task	old word-old word pair condition	WM	2
Arnow et al., 2002	20	20	24	Affective video viewing	erotic > sports	E	4
Arnow et al., 2009	14	0	24	Affective video viewing	turgidity	E	5
Arsalidou et al., 2010	10	6	35.4 ± 7.7	Face processing task	father > celebrity male	E	1
Bach et al., 2008	16	8	26 ± 3.9	Emotion discrimination task	anger > fear	E	3
Bapi et al., 2006	10	5	21.5	Finger motor task	motor > follow: Early Stages	BM	5
Bartels and Zeki, 2000	17	11	24.5	Face processing task	partner > friend	E	4
Baumann et al., 2010	17	0	31.6 ± 7.4	Spatial memory task	retrieval phase: experimental > baseline	WM	2
Baumgartner et al., 2006	9	9	24.78 ± 2.9	Mood induction task	combined > picture	E	2
Bengtsson et al., 2004	7	2	21.5	Finger motor task	main effect: Long ordinal structure	BM	7
Berns et al., 2001	25	n/r	33	Predictability task	unpredictable > predictable	S	1
Beudel et al., 2009	18	9	27 ± 8.4	Speed discrimination task	speed > place at stop (4 vs 3)	WM	2
Boehler et al., 2010	15	9	22.9	Stop-signal task	successful stop trial > go trial	EF	2
Bray et al., 2008	23	6	24 ± 5.3	Stimulus response task	outcome-specific transfer: Pavlovian cue > incompatible option	R	3
Brovelli et al., 2008	14	7	26	Visuomotor learning	absolute prediction error	EF	2
Bueti et al., 2008	14	10	25 ± 5.2	Perception task	perception condition > control	WM	3
				Action task	action condition > control	BM	3
Butler et al., 2007	42	16	28 ± 6	Threat anticipation task	threat > safety	E	4
Camara et al., 2010	35	24	21.8 ± 2.2	Gambling task	gain > loss	R	1
Campbell et al., 2007	16	8	23 ± 3.1	Pre-pulse inhibition task	pre-pulse inhibition	BM	2
Canessa et al., 2005	55	26	22.7	Reasoning task	social exchange > baseline	E	1
Caramia et al., 2010	15	11	36.5 ± 10.4	Finger-to-thumb opposition	task > control	BM	1
Cerasa et al., 2005	12	0	24.9 ± 2.7	Motor synchronization task	visually cued motor synchronization task > conventional-baseline	BM	4
Chan et al., 2008	11	n/r	26.5	Lexical decision task	English: verb > fixation	WM	1
Chan et al., 2009	22	10	24.5	Rhymes task	rhyme > filtered sound	WM	2
Chao et al., 2009	65	33	35	Stop-signal task	short > long SSRT sessions	EF	1
Chen and Desmond, 2005	15	7	22.53 ± 2.7	Sternberg task	maintenance	WM	3
Chevrier et al., 2007	14	6	29.4	Stop-signal task	successful stop-phase	EF	1
Choi et al., 2001	10	5	30	Pantomime tool-use task	finger tapping > fixation: Right Hand	BM	1
Christensen et al., 2006	13	5	31.5	Graded visual perception task	clear perceptual experience > vague perceptual experience and clear perceptual experience > no perceptual experience	WM	9
Chua et al., 2009	29	13	20.2 ± 1.08	Gambling task	winning > losing	R	2
Ciesielski et al., 2006	10	5	23.5 ± 2.29	Categorical n-back task	categorical n-back	WM	1
Colibazzi et al., 2010	10	5	25.51 ± 4.58	Mood induction task	correlation w/ arousal rating	E	2
Cox et al., 2005	22	10	24	Conditioning task	conditioning task: reward > negative feedback	R	2
Crescentini et al., 2010	14	8	30.5 ± 4.5	Response selection task	high selection and strong association nouns > low selection and strong association nouns	WM	4
Daselaar et al., 2003	26	0	32.5	Serial reaction time task	fixed > random	BM	4

TABLE I. (Continued)

Author-year	Participants *N*	Participants F	Participants Age (M ± SD)	Task	Contrast	Category	Foci
Debaere et al., 2004	12	7	26.5	Wrist motor task	coordination > single limbs	BM	2
den Ouden et al., 2009	16	8	25.3 ± 3.3	Associative learning task	conditioning stimulus presence x visual outcome x Rescorla-Wagner learning (restricted to positive conditioning stimulus)	WM	7
de Rover et al., 2008	6	3	27 ± 3.6	Retrieval task	temporal > spatial	WM	6
Diekhof et al., 2009	9	5	24.4 ± 2.2	Auditory discrimination task	detected deviancy > implicit baseline: correct detection of deviancy and false alarms	WM	2
Dong et al., 2000	10	3	26.4 ± 4.5	Lexical decision task	Japanese kana mirror reading > normal reading	WM	1
Dreher et al., 2008	20	10	25 ± 3.7	Gambling task	anticipation of rewards	R	2
Epstein et al., 2005	12	8	22.5#	Navigation task	correlation between Santa Barbara sense of direction score and viewpoint-specific	WM	2
Erk et al., 2002	12	0	31.4 ± 6.9	Socio-cultural influence task	sports cars > small cars	E	1
Erk et al., 2005	10	3	23.5	Emotion influence task	memory: negative successful recognition effect	E	2
Erk et al., 2010	16	16	23.8 ± 2.8	Long-term emotion influence	recognition effects: main memory effect	WM	1
Ernst et al., 2004	17	n/r	30	Wheel of fortune task	anticipation: monetary > control	R	2
Ettlin et al., 2009	17	7	35.5	Dental pain perception task	correlation w/ intensity rating	S	1
Fiddick et al., 2005	24	12	26.3	Reasoning task	reasoning_precautions > reasoning_social contracts	WM	2
				Reasoning task	reasoning_social contracts > reasoning_precautions	E	1
Fink et al., 2002	12	1	27 ± 7.5	Line bisection judgment task	line center judgements > non visuospatilal and line length comparisons > non visuospatial baselines)	WM	1
Forstmann et al., 2010	17	9	25.2 ± 3.01	Perceptual decision making	reliable > neutral	WM	2
Francis et al., 2009	14	5	30 ± 7	Ankle motor task	active > rest	BM	2
Francois-Brosseau et al., 2009	14	7	22.6 ± 0.5	Finger motor task	self-initiated > control: right hand	BM	4
Gandini et al., 2008	13	6	26	Quantification strategy task	anchoring > control	WM	2
Gheysen et al., 2010	22	17	22	Visio-motor task	random > sequence: first session	WM	1
Goel et al., 2000	11	4	29.4 ± 7.2	Syllogistic reasoning task	reasoning	EF	2
Gur et al., 2007	36	19	30.1 ± 8.3	Target detection task	target	WM	1
Guroglu et al., 2008	28	20	22.6 ± 2.04	Social interaction stimulation	relationship x emotional valence	E	1
Habas and Cabanis, 2007	9	n/r	30	Finger motor task	nondiscrimination motor task	BM	2
Habas and Cabanis, 2008	7	n/r	25	Finger motor task	discrete > continuous movements	BM	2
Hall et al., 2010	6	6	35	Ramp-tonic visceral pain task	suprathreshold > subthreshold distention intervals	S	1
Hardin et al., 2009	18	n/r	29 ± 4.8	Wheel of fortune task	most extreme outcome in the positive context > most extreme outcome in the negative context	R	2
Haslinger et al., 2002	8	1	26 ± 2.83	Finger motor task	finger movements regardless of complexity	BM	1
Herwig et al., 2007	12	12	27.5	Emotion task	expect neg>neu and expect neg>pos	E	1
Hofer et al., 2007	21	0	32.8 ± 7.5	Encoding task	object encoding > reference condition	WM	1
Hsu et al., 2009	21	11	29.6 ± 7.5	Gambling task	correlations w/ probability term	R	9
Huettel and Misiurek, 2004	14	10	26 ± 8	Target detection task	target	WM	2
Huettel et al., 2004	8	5	23	Target detection task	target > nontargets	WM	1

TABLE I. (Continued)

		Participants					
Author-year	*N*	F	Age (M ± SD)	Task	Contrast	Category	Foci
Iyer et al., 2010	17	10	22	Gambling task	outcome: reward > punishment	R	5
				Gambling task	cue: absolute value, subjective performance	WM	5
Izuma et al., 2008	19	10	21.6 ± 1.5	Gambling task	(self>other) x (high social reward>no social reward)	E	4
Jahn et al., 2004	13	7	27.3	Motor imagery task	walking > lying	BM	1
Jamadar et al., 2010	18	11	25 ± 7	Cued task-switching paradigm	informatively cued (go) > no-go	WM	2
Janzen and Weststeijn, 2007	15	7	22.6	Recognition task	in-route items > against-route items	WM	1
Kaffenberger et al., 2010	16	8	27.6 ± 3.6	Emotion expectation task	(presentation of positive pictures after an ambiguous cue > positive pictures after unambiguous positive cue) > (presentation of negative pictures after an ambiguous cue > negative pictures after unambiguous negative cue)	E	2
Kang et al., 2009	19	5	21.7 ± 3.5	Epistemic curiosity task	answers revealed: subject's prior guess had been incorrect vs correct	WM	2
Kikyo and Miyashita, 2004	15	5	26	Recall–Judgment–Recognition	correlations w/ feelings of knowing	WM	4
Kim et al., 2010	30	12	27.3 ± 3.7	Scene processing task	rural > urban	WM	3
Kimmig et al., 2008	12	6	28 ± 5	Visual pursuit task	visuo-oculomotor stimulation > visual stimulation	EM	6
Kirsch et al., 2003	27	24	23.3	Differential conditioning task	monetary visual cue > control visual cue	R	6
Koch et al., 2008	28	17	24.6 ± 5.5	Trial-and-error learning task	positive feedback/reward	R	2
Konrad et al., 2008	24	12	34	Synonym generation task	synonym generation task: Women (mid-luteal phase of menstrual cycle)	WM	2
				Synonym generation task	synonym generation task: Men	WM	2
Kosson et al., 2006	19	9	30.7	Passive avoidance task	post-criterion correct responses > incorrect responses made throughout the task	EF	3
Koylu et al., 2006	35	n/r	28.3 ± 5.2	Semantic memory task	semantic > tone decision	WM	1
Kuhn and Brass, 2009	17	9	21.6	Modified stop task	decide-go > stop condition	WM	2
Kumar et al., 2010	12	5	28.4 ± 3.2	Phrase reading	English(2nd language) > Hindi(1st language)	WM	1
Kumari et al., 2007a	14	0	32.13 ± 7.47	Fear induction task	shock-II > safe	E	4
Kumari et al., 2007b	12	0	36.25 ± 11.12	Prepulse inhibition task	pre-pulse-inhibition: 120-ms stimulus onset asynchrony > pulse-alone	S	1
Kuperberg et al., 2008	16	5	42 ± 9	Sentence comprehension	animacy > pragmatic	EF	4
Landmann et al., 2007	16	0	23 ± 2.2	Motor trial-and-error learning task	chance discovery > logical discovery	WM	1
				Motor trial-and-error learning task	feedback parameters: prediction error	R	3
Lee et al., 2006	20	0	25.09 ± 5.34	Visual object discrimination	object change > no change	WM	2
Liddle et al., 2006	28	7	28.2 ± 8.9	Target detection task	target stimulus processing > novel stimulus processing	WM	2
Lie et al., 2006	12	2	24 ± 5	Wisconsin card sorting task	task A: no instruction of dimension > high-level baseline	WM	1
Lieberman et al., 2004	9	5	26	Artificial grammar task	grammatical > nongrammatical: all items	WM	2

TABLE I. (Continued)

Author-year	Participants			Task	Contrast	Category	Foci
	N	F	Age (M ± SD)				
Lin et al., 2008	24	16	21 ± 3.1	Iowa gambling task	anticipation period	R	2
Linke et al., 2010	33	16	22.64 ± 2.92	Probabilistic reversal learning task	reward > punishment	R	8
Liu et al., 2010	24	12	21.8 ± 2.15	Bilingual naming task	naming in Chinese and English	WM	3
Longe et al., 2010	17	17	24.71 ± 4.21	Self-criticism and self-assurance task	self-criticism during threat to self scenarios > neutral scenarios	E	2
Macar et al., 2004	13	6	39.5	Time and force production	time task > baseline	WM	2
				Time and force production	force task > baseline	BM	2
Mainero et al., 2004	22	14	36	Paced Auditory Serial Addition Test	paced auditory serial addition task	WM	4
Manoach et al., 2003	12	6	29.7 ± 6.9	Sternberg task	probe	WM	1
Marchand et al., 2007	15	0	48.2 ± 11.6	Paced motor task	synchronized motor task: right > left	BM	1
Marco-Pallares et al., 2007	12	8	23.5	Feedback processing task	positive > negative feedback trials	R	2
Marklund et al., 2007	16	8	30.5	N-back task	high- > low- load	WM	1
Marques et al., 2009	21	12	26.09 ± 1.89	Sentence feature verification	true and false statements	WM	4
Marvel and Desmond, 2010	16	10	23.69	Sternberg task	maintenance	WM	2
Marx et al., 2004	14	7	25.4	Open/close eyes	fixation LED > eyes closed	EM	2
Matsuda et al., 2004	21	n/r	39.2 ± 10.2	Saccade task	saccade > rest	EM	3
Mayer et al., 2009	16	8	27.3 ± 7.43	Bottom-up auditory orienting	invalid > valid at 200ms	WM	2
Melcher and Gruber, 2006	12	6	25.67 ± 1.88	Oddball tasks	color-oddballs and word oddballs	WM	1
Menon et al., 2000	16	8	20.28	Arithmetic task	3sec 3-operand	WM	2
Menon et al., 2001	14	6	23.6 ± 7.2	Go/NoGo task	response inhibition	WM	2
Meschyan and Hernandez, 2006	12	7	22.3 ± 1.35	Bilingual word-reading task	Spanish (1st language) > rest	WM	1
Meseguer et al., 2007	14	0	28.8	Vowel-consonant/Emotion	positive > neutral	E	3
Mestres-Misse et al., 2010	21	11	24 ± 1.8	Word-meaning task	word exposure x type of word	WM	4
Michels et al., 2010a	16	8	24.8 ± 3.8	Sternberg task	5 consonants > 2 consonants	WM	2
Michels et al., 2010b	13	13	26	Clitoral stimulation	clitoral stimulation	S	2
Mobbs et al., 2003	16	9	22.4 ± 1.8	Cartoon task	funny > nonfunny cartoons	E	1
Monchi et al., 2001	11	6	24	Wisconsin card sorting task	negative feedback > control feedback	EF	2
Monchi et al., 2007	7	n/r	51.1	Wisconsin card sorting task	retrieval with shift > retrieval without shift	WM	4
Munzert et al., 2008	10	10	24.1 ± 1.8	Observing and imagining motion	observational and motor imagery	BM	2
Murray et al., 2008	12	3	26 ± 3	Reward prediction task	prediction error on reward trials > prediction error on neutral trials	R	3
Na et al., 2009	12	0	33.6 ± 6.2	Electroacupuncture stimulation	real electroacupuncture left leg > rest	S	6
Nagel et al., 2008	21	0	29.4 ± 5.2	Foveopetal step-ramp paradigm	condition A: continuous target presentation	EM	5
Nakai et al., 2003	10	5	32.5	Finger motor task	TATA (combination of the internal conversion) – 05	BM	1
Nieuwenhuis et al., 2005a	14	6	25.4	Gambling task	highest outcome > lowest outcome (+60c vs. 40c)	R	3
Nieuwenhuis et al., 2005b	14	13	21.9	Time estimation task	positive > negative feedback trials	R	2
Nishimura et al., 2009	16	8	24.5	Tool-use task	real vs. simulation of the right hand	BM	1
Nomura et al., 2007	34	19	23	Category-learning task	information integration-group: correct > incorrect	EF	3

TABLE I. (Continued)

Author-year	Participants			Task	Contrast	Category	Foci
	N	F	Age (M ± SD)				
Numminen et al., 2004	11	6	27.9	Tactile comparison task	task > rest TR 7	S	4
Ogg et al., 2008	30	17	24.2	Conners' CPT task	continued performance test	WM	2
Oh and Leung, 2010	12	6	22.6	Delayed recognition task	cue period	WM	4
Parkinson et al., 2009	11	3	28 ± 10	Arm motor task	right arm voluntary movement	BM	3
Parris et al., 2007	22	13	25	Rule switching task	flip > hold: experiment 1	EF	3
Pastor et al., 2004	14	n/r	28.9 ± 5.1	Discrimination tasks	discrimination > detection	S	2
Petit et al., 2009	27	12	22	Visually guided saccades	large and small visually guided saccades > central fixation	EM	2
Phan et al., 2010	36	22	30.03 ± 8.64	Trust task	trust: reciprocate > trust: defect	EF	2
Provost et al., 2010	13	7	24.6 ± 2.3	Monitoring task	self-ordered monitoring > recognition condition	WM	3
Qin et al., 2007	20	18	22 ± 4	Memory formation task	hit discontinuous associations > hit simultaneous associations	WM	2
Rameson et al., 2010	17	9	19.5	Self-reference task	explicit processing of self-relevant information	EF	4
Rao et al., 2008	14	6	25.1	Balloon analog risk task	correlations w/ voluntary risk	R	8
Rauchs et al., 2008	16	8	22.1	Navigation task	recognition > impoverished	WM	2
Reiss et al., 2008	12	7	25.9 ± 4.1	Cartoon task	humorous > nonhumorous	E	1
Remijnse et al., 2005	27	19	32	Reversal learning task	main effect of reward (correct response > neutral baseline)	R	4
Remy et al., 2008	12	6	23.6 ± 3.6	Wrist motor task	pre-post changes: 90F pattern	BM	1
Reske et al., 2010	15	15	36.8 ± 7.66	Smelling task	rotten yeast > ambient air	E	2
Reverberi et al., 2010	26	11	25 ± 5	Reasoning task	syllogistic problems	WM	1
Rissman et al., 2003	15	8	22.9 ± 6.5	Lexical decision task	unrelated > related	WM	1
Rocca et al., 2007	15	9	21	Hand-foot motor task	anterior > posterior position: right upper limb	BM	1
Rodriguez-Moreno and Hirsch, 2009	12	9	26.6 ± 5.6	Weather prediction task	visual and auditory modalities conjoined (reasoning > control): Conclusion	WM	2
Sakamoto et al., 2009	14	8	24.3	Tongue motor task	tongue movement	BM	2
Sambataro et al., 2006	24	13	26.8 ± 5.6	Facial emotion task	contempt > neutral	E	2
Schilbach et al., 2010	21	0	24	Self/other task	self > other	E	1
Schneider et al., 2008	15	7	24.4 ± 2.72	Emotion face task	picture high self picture low self > baseline high self baseline low self	E	1
Schulz-Stubner et al., 2004	12	n/r	n/r	Pain perception task	painful stimuli without hypnosis	S	2
Seidler et al., 2004	12	4	25.1	Hand motor task	motor task	BM	1
Seidler et al., 2006	26	13	23.4 ± 3.9, 24.3 ± 5.0	Joystick aiming task	adaptation > baseline: more activation for the first adaptive block	BM	4
Seseke et al., 2006	11	11	30.0±6.9	Pelvic motor task	relaxation and contraction of pelvic floor muscles	BM	2
Shibata et al., 2010	13	3	23.8	Literal sentence task	literal sentence condition	EF	3
Shih et al., 2009	17	8	23.8±3.5	Duration discrimination task	common activations	WM	1
Simon et al., 2010	24	13	24.8±3.2	Monetary incentive delay task	anticipation of reward > nonreward	R	3
Sinke et al., 2010	14	7	23.6 ± 5.1	Color and emotion naming	color > emotion naming	WM	2
				Color and emotion naming	threat > tease	E	2

TABLE I. (Continued)

Author-year	Participants *N*	F	Age (M ± SD)	Task	Contrast	Category	Foci
Smith et al., 2009	25	12	29.1 ± 5.5	Go/NoGo task	high magnitude > low-magnitude selections	R	1
Snijders et al., 2009	28	14	26.5	Sentence comprehension	ambiguous > unambiguous conditions	WM	3
Stevenson et al., 2009	11	6	26.5	Multi-sensory interactions	experiment 1: Δaudio + Δvisual < Δaudio-visual indirect inverse effectiveness	S	2
Straube and Chatterjee, 2010	16	7	25.9 ± 3.6	Causality judgment task	correlations w/time delay in relation to predictive value of time for judgment of causality	EF	1
Sung et al., 2007	12	0	24 ± 3.4	Thermal stimulation	conjunction analysis	S	1
Szameitat et al., 2007	15	6	28	Motor imagery task	imagery > resting baseline [(upper extremity + whole body)/2–resting baseline]	BM	2
Takahashi et al., 2004	15	6	29.1 ± 7.8	Emotion-induction task	unpleasant > neutral	E	1
Takashima et al., 2007	21	11	23.3 ± 4.8	Paired associate task	stabilized and labile contrast to nonmemory condition	WM	4
Takeichi et al., 2010	23	12	24.75	Speech comprehension	nonmodulated speech > modulated speech (nonmodulated forward –modulated forward)+(nonmodulated reversed–modulated reversed)	WM	1
Tanaka et al., 2006	18	5	n/r	Markov decision task	regular	R	7
Tinaz et al., 2006	12	6	21.75 ± 4	Picture sequencing task	picture sequencing task > object discrimination control task	EF	2
Tobler et al., 2007	16	8	27	Monetary reward task	expected value	R	5
Tomasi et al., 2005	30	15	31 ± 9	Sequential letter tasks	quiet 1-back	WM	2
Tunik et al., 2009	18	9	21.8 ± 2.6	Corrective motor task	activation related to the task	BM	2
van den Heuvel et al., 2005	22	11	29.9	Tower of London task	planning > baseline	EF	2
Vanhaudenhuyse et al., 2009	13	5	24 ± 2	Pain perception task	pain during normal wakefulness	S	2
von Zerssen et al., 2001	12	6	27	Explicit memory task	correct old answers (old-OLD) > correct new answers (new-NEW)	EF	4
Vrticka et al., 2008	16	8	23.6 ± 3.6	Social visual dot-counting task	won > lost	R	4
Wagner et al., 2008	12	7	33.5	Motor imagery task	locomotion-stand	BM	2
Walsh and Phillips, 2010	20	10	25 ± 5.2	Outcome-anticipation task	x > fixation	WM	3
Walter et al., 2008	21	10	24.82	Emotion-erotic pictures	positive bodily > positive nonbodily	E	2
Wang et al., 2007	12	6	19.5	Bilingual language-switching	language switching > language nonswitching	EF	1
Wang et al., 2008	12	6	21.5	Motor imagery task	hand image > rest	BM	1
Weber and Huettel, 2008	23	11	23	Decision making task	predicts choice of riskier option	R	1
Welander-Vatn et al., 2009	28	17	38.1 ± 10.8	Go/NoGo task	task > rest	WM	1
Westen et al., 2006	30	0	38.5	Reasoning task	post-decision judgment: consider1 > consider2 for same-party targets	EF	1
Wiese et al., 2004	20	11	32.7 ± 9.3	Finger motor task	self-initiated movements > externally triggered movements	BM	1
Wilkinson et al., 2001	12	6	30	Global/Local judgments	internal > external	EF	2

TABLE I. (Continued)

	Participants						
Author-year	*N*	F	Age (M ± SD)	Task	Contrast	Category	Foci
Williams et al., 2005	12	0	23.5	Joint dot-tracking task	joint > nonjoint attention	WM	2
				Joint dot-tracking task	joint attention > rest	EM	3
Wittfoth et al., 2010	20	10	24.9 ± 3.7	Emotional prosody task	[negative prosody positive content > (positive prosody negative content + positive prosody positive content)]	E	1
Wittmann et al., 2008	25	12	24.0 ± 2.0	Rewarded number comparison task	reward-predicting stimuli > nonreward-predicting stimuli	R	3
Wolbers et al., 2006	11	3	26	Subliminal prime task	valid / invalid > fixation	WM	3
Wolf and Walter, 2005	15	7	28.13 ± 4.17	Sternberg task	load 3 > load2	WM	2
Wolf et al., 2008	21	10	28.6 ± 7.1	Sternberg task	target	WM	4
Woodward et al., 2006	12	4	34.5 ± 10.03	Stroop task	incongruent word reading	EF	3
Wu et al., 2004	12	4	30.5	Finger motor task	sequence-12 task: before-training condition > after-training stage	BM	1
Xue et al., 2009	13	5	23.6 ± 6	The cups task	win > loss: across both risky and safe choices	R	7
Yoo et al., 2003	13	5	29.5	Tactile imagery task	imagery > stimulation	S	2
Zago et al., 2008	14	8	23.5	Working memory tasks	number manipulation > maintenance	WM	2
Zeki and Romaya, 2008	17	7	34.8	Emotion face task	hated faces > neutral faces	E	1
Zijlstra et al., 2009	17	0	40.4 ± 10	Affective pictures	pleasant > baseline	E	5
Zink et al., 2004	16	6	25	Rewarded target detection	active money > passive money	R	3
Zysset et al., 2006	15	7	26.6	Simple decision-making task	parametric contrast for similarity between alternatives	WM	2

Note: A total of 3,518 participants took part in these studies, 11 studies did not report gender; of the remaining 45.3% were female (F) participants. The majority of studies that reported handedness (82%) tested primarily right handed participants (99%). With the exception of two studies, the majority reported age of the participants (# median age), whose average age was 26.9 ± 4.9. Contrasts were categorized into seven groups based on the task description. Motor functions were grouped into body movements (BM) and eye movements (EM); Cognitive functions were categorized into working-memory (WM) that included tasks such as the n-back, Sternberg, as well as encoding and retrieval of material, and executive functions (EF) that included strategy planning and formation such as judgment and switching tasks; Affective functions were categorized into emotion (E) and reward (R) groups, which included eliciting and judging emotion, and receiving feedback including monetary reward, respectively; lastly, somatosensory (S) functions included contrasts related to pain and other kinesthetic stimulation.

Meta-Analyses

ALE is a coordinate-based meta-analytic method [Laird et al., 2005; Turkeltaub et al., 2002; Eickhoff et al., 2009] available through BrainMap (http://brainmap.org/ale/; Research Imaging Center of the University of Texas in San Antonio). Contrast coordinates (i.e., foci) from different studies are used to generate 3D maps describing the likelihood of activation within a given voxel in a template MRI [Laird et al., 2009]. Significant findings are based on whether the data are more likely to occur compared to a random spatial distribution.

Coordinates from source datasets were first transformed into common space. MNI coordinates were transformed into Talairach space using the best-fit MNI-to-Talairach transformation [Lancaster et al., 2007]. To maintain data independence, each meta-analysis contained foci from only one contrast per study. The 5-category model by Alexander et al., [1990] was expanded to a 7-category model. We retained the scheme of Alexander et al. [1990] for cognitive and motor functions. However, the cognitive processes we have termed "working memory" and "executive functions", were created to correspond with the "dorsolateral" and "lateral orbitofrontal'' systems of Alexander et al. [1990]. Similarly, motor movements were separated into body and oculomotor (eye movement) categories. Whereas Alexander et al., [1990] grouped emotion and reward processes as the "limbic system", we divided these studies into separate categories. We also added a new category of somatosensation.

The criteria for grouping coordinates into the seven categories were as follows: Motor functions were separated into body and eye movements. Body movements were activation foci associated with any movements of the hands, legs, fingers, etc., whereas eye movements were mainly evoked by saccade or anti-saccade tasks. Cognitive functions were categorized separately into working-memory and executive functions. Although tasks that engage executive functions often incorporate a component of working-memory, we chose to categorize executive function studies separately to be consistent with the model of Alexander et al. [1990] and to have a reference point for purposes of comparison. The working memory category included tasks that required encoding, storing, manipulating and retrieving information (e.g., n-back tasks, Sternberg tasks). Executive functions included tasks that required strategy planning and strategy formation (e.g., judgment and switching tasks). Affective functions were categorized into emotion and reward processes. Emotional functions included tasks that required any form of either eliciting or judging emotion. Reward functions included tasks that involved receiving positive or negative feedback and any type of task-related reward. Last, somatosensory functions included activation evoked by stimuli (noxious and/or innocuous) applied to the body. In cases where contrasts involved multiple categories tapping two or more processes within our categorization scheme (i.e., working memory and executive functioning) the original task description was compared with our criteria to identify the primary function being assessed. For example, a task could require working memory processes within the context of decision making. However, if the contrast reflected encoding, storing, maintaining or retrieving information then it would be classified as working memory. Table I provides details on all of the source datasets that were included in the analyses.

The data were subjected to random-effects analyses using GingerALE v2.1 [Eickhoff et al., 2009]. Using this method, activation foci from each study are converted into three-dimensional Gaussian probability functions. This process involves smoothing the data using a Gaussian blurring kernel. The full-width at half maximum (FWHM) size of the Gaussian blurring kernel is based on the number of participants used in each contrast. Median FWHM values across the included studies by category were: body movements = 9.75, eye movements = 9.57 working-memory = 9.43, executive = 9.50, emotion = 9.43, reward = 9.23, sensory = 9.75. A voxel-wise likelihood of activation was calculated and was corrected for multiple comparisons using the false discovery rate (FDR) $q = 0.001$. A conjunction process was employed to display results from the ALE maps associated with the different functions, using AFNI [Cox, 1996]. Activation likelihood estimates of functional categories (e.g., affective processes: emotion and reward) were overlaid and displayed on a template MRI using the program 3dcalc; spatial overlap was illustrated by a common color.

To assess hemispheric dominance for activation associated with the seven categories of interest, laterality indices were calculated using AFNI. Regions-of-interest were anatomically defined using an AFNI template [MNI N27 brain in Talairach space (Eickhoff et al., 2007)]. The masks were applied to the thresholded ALE maps and hemispheric dominance was calculated in each region. A laterality index (LI = [Left − Right] / [Left + Right]) of >0.20 was deemed left dominant and <-0.20 right dominant; values in between were considered bilateral.

RESULTS

The data from 204 fMRI datasets were included in the meta-analyses. Figure 1 shows the number of studies per year included in the meta-analyses as well as the number of studies and foci related to each function. A total of 3,518 participants (99% right handed) took part in these studies; 45.3% were female. The average age ranged between 19.5 and 51.1 years with most participants being around 25 (mode = 24, median = 25.51, mean 26.94 ± 4.93 years; for more details on the source datasets see Table I).

Peak foci showing concordance across studies are shown in Table II (corrected for multiple comparisons using the false discovery rate, $q = 0.001$). Figure 2 illustrates the location and spatial extent of significant concordance in

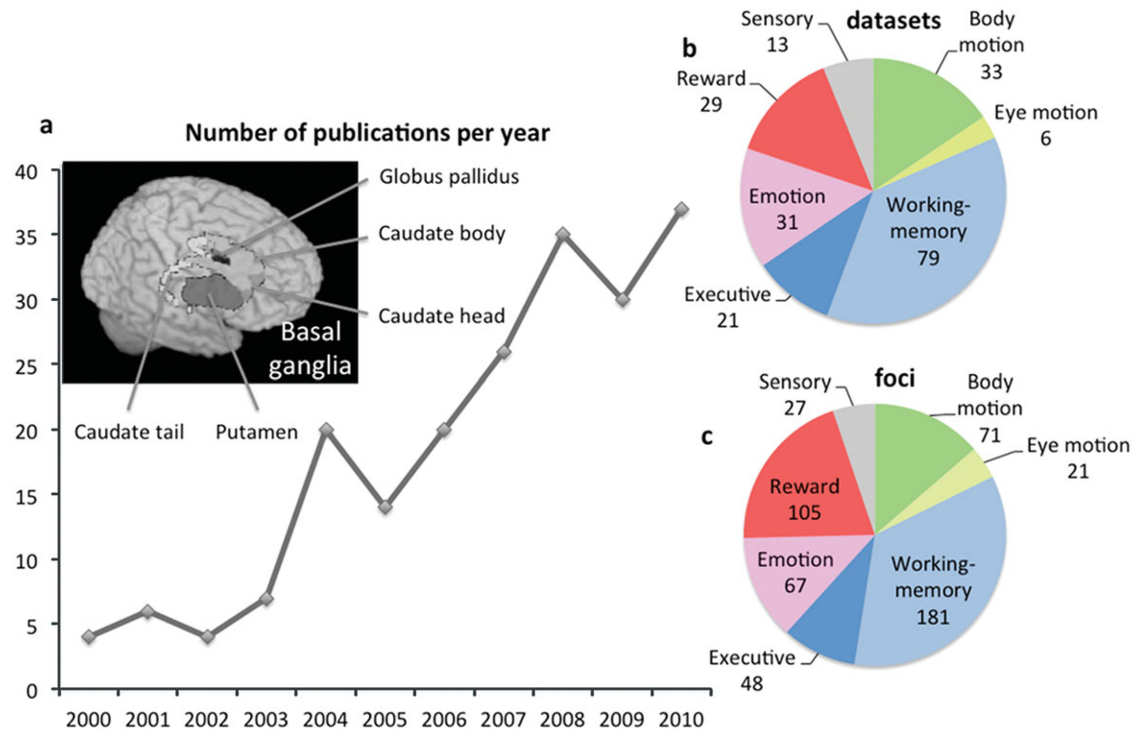

Figure 1.

Source datasets. (**a**) Number of fMRI studies that reported activity on basal ganglia and passed selection criteria as a function of year, (**b**) the distribution of datasets, and (**c**) number of foci that contributed to the analysis of each functional category. A single contrast from each study was selected for a category; in a few instances two contrasts were selected and entered in different categories (e.g., a contrast for reward and working-memory categories; see Table I for more details on functional categorization of contrast and selection).

each category observed across studies. We also illustrate the overlap for motor, cognitive and affective categories (Fig. 3). Figure 4 portrays laterality proportions as well as laterality indices associated with each function by basal ganglia structure. We highlight four main findings, discussed in detail below:

a. Motor processes occupied central basal ganglia structures (putamen and globus pallidus); eye movements were left lateralized, whereas body movements were either bilateral or right dominant in the putamen and globus pallidus;
b. Working-memory processes (encoding, storing, manipulating, and retrieving information) elicited the most widespread responses, which were the least lateralized; executive processes (e.g., planning and task switching) were anterior and ventral to those elicited by working-memory processes;
c. Reward processes evoked activity in the anterior parts of the caudate head and overlapped most extensively with emotional processes in the left hemisphere, which suggests differential hemispheric contributions (Fig. 3).
d. Somatosensory processing, particularly pain, showed preferential activation in the dorsal putamen.

DISCUSSION

For decades, our knowledge of the basal ganglia has been largely limited to lesion and animal studies. We used neuroimaging data from healthy, human participants to create a new cohesive topographical model of the functions of the basal ganglia. The results provide novel insight into the role of the basal ganglia in motor, cognitive, affective, and somatosensory processing.

Body movements showed significant concordance across studies in central areas of the basal ganglia bilaterally with the highest likelihood of activation in the left putamen. Eye movements also had a significant likelihood of activating the putamen, but ventral to the activation evoked by body movements; indices of hemispheric dominance showed that eye movements were left lateralized. Previous reviews on movement disorders proposed that the putamen was essential for learning novel, complex, and

TABLE II. Concordant basal ganglia substructures as a function of functional category

	Area	x	y	z	ALE Value	Volume (mm^3)
Body motion						
	L. Putamen	−22	−4	14	0.036	5312
	L. Putamen	−24	−6	4	0.027	
	R. Lateral Globus Pallidus	22	−6	2	0.033	5224
	R. Putamen	22	6	14	0.025	
	L. Caudate Body	−6	8	8	0.016	176
	R. Caudate Body	2	16	8	0.014	72
Eye motion						
	L. Putamen	−20	2	6	0.031	936
	R. Putamen	20	6	4	0.020	160
Working−memory						
	L. Putamen	−14	6	6	0.070	23768
	R. Putamen	16	6	6	0.065	
	L. Lateral Globus Pallidus	−26	−14	−2	0.025	
Executive						
	R. Caudate Head	12	10	2	0.038	2880
	L. Putamen	−14	8	2	0.036	2512
	R. Putamen	24	−6	4	0.022	352
	L. Caudate Body	−18	−16	22	0.014	16
	R. Caudate Body	16	−12	26	0.014	16
Emotion						
	L. Caudate Body	−10	8	6	0.035	5296
	L. Caudate Body	−16	2	14	0.029	
	L. Medial Globus Pallidus	−14	−2	−2	0.022	
	L. Putamen	−22	16	4	0.017	
	R. Caudate Body	12	2	18	0.024	2304
	R. Caudate Body	10	8	12	0.023	
	R. Putamen	18	4	6	0.022	
Reward						
	L. Caudate Head	−10	6	0	0.063	4240
	L. Lateral Globus Pallidus	−12	6	−4	0.062	
	L. Putamen	−16	8	−6	0.061	
	R. Lateral Globus Pallidus	12	6	0	0.062	2832
Sensory						
	L. Putamen	−26	6	−4	0.019	424
	R. Caudate Body	10	8	8	0.012	128
	L. Caudate Body	−10	8	10	0.012	56

Coordinates (x, y, z) are in Talairach space using FDR ($q = 0.001$); L, Left; R, Right; ALE, activation likelihood estimate.

voluntary movements [Bartels and Leenders, 2008; Ceballos-Baumann, 2003], but less important for automated, well learned movements [Ceballos-Baumann, 2003]. In line with these claims, we showed concordance of activity in the putamen for body movements and also provided spatially specific coordinates as they were evoked in the healthy basal ganglia. In addition, we distinguished eye movements from body movements. Eye movements, a subdivision of motor movements, were previously related to basal ganglia activity, whether these were voluntary saccades [Leigh and Kennard, 2004; Sweeney et al., 2007] or anti-saccades [Dillon and Pizzagalli, 2007]; the information provided by these studies was not spatially specific. In contrast to our results, Alexander et al., [1990] proposed that the putamen and the globus pallidus mediated body movements and that eye movements primarily recruited the caudate body and the globus pallidus. For eye movements, we found no evidence of peak concordance in the globus pallidus or in the caudate body, but rather in the anterior putamen. Thus, the current analytical approach based on quantitative data, both complements and extends previous qualitative reviews by providing new information on the spatial extent and lateralization of body and eye movements subserved by specific basal ganglia nuclei.

The model by Alexander et al., [1990] distinguished between working-memory processes, subserved by the dorsolateral prefrontal cortex (Brodmann areas 9 and 10), and executive functioning, processed by the lateral orbitofrontal cortex (Brodmann area 10). They suggested that working-memory processes would recruit the dorsolateral caudate head and continue rostrocaudally to posterior regions, whereas the executive functions would implicate the ventromedial sector of the caudate head and extend to posterior structures just medial to those involved in

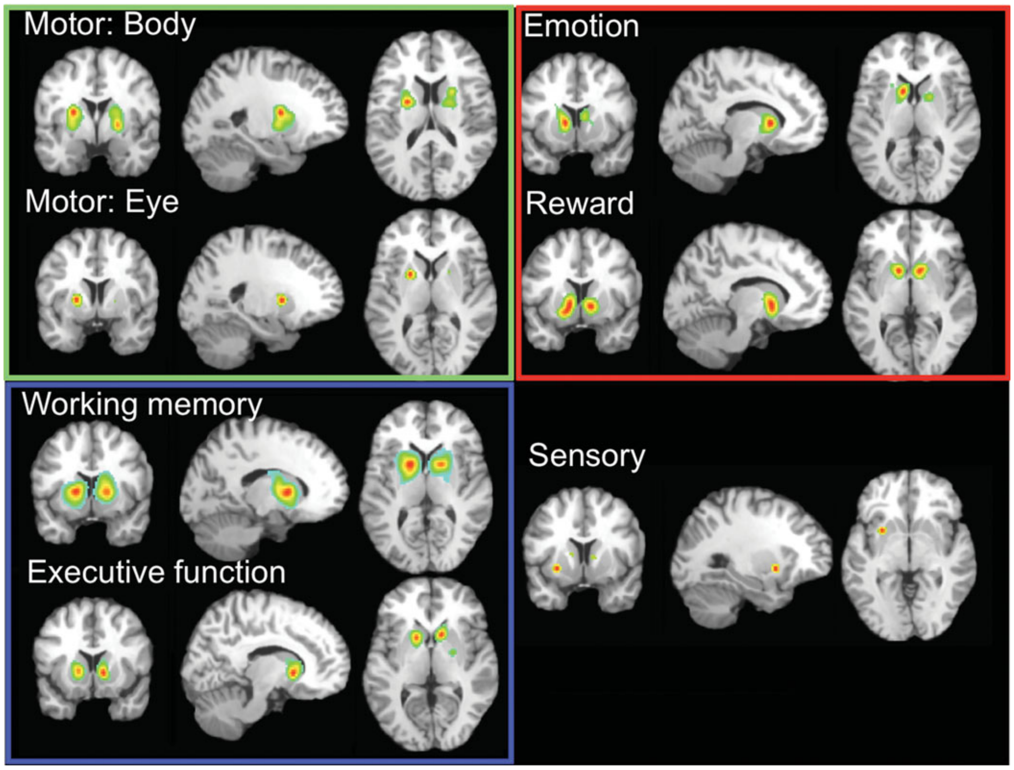

Figure 2.

Brain maps demonstrating significant concordance across studies centered over the peak ALE value for each category. A voxel-wise likelihood of activation was determined using false discovery rate (FDR) $q = 0.001$ multiple comparison control. Left = Left.

working-memory. Our data showed that working-memory processes (maintaining and manipulating information) recruited large areas of the basal ganglia primarily centered over the anterior putamen, while executive functions (e.g., planning and set-shifting) activated the head of the caudate nucleus. Additionally, working-memory processes were either left dominant or bilateral and executive processes were right lateralized (head and body of the caudate).

In relation to findings of lateralization of working memory processes in the cortex, nonhuman primate studies [Parker and Gaffan, 1998] and some human imaging studies [Petrides et al., 1993] have noted differential hemispheric processing of verbal and spatial tasks, with the former type involving the left hemisphere and the latter right hemisphere processes. In our classification scheme of working memory tasks, divisions between verbal and spatial tasks were not created. Rather the goal of this study was to examine broad working memory processing in the basal ganglia; however, future research could assess the lateralization of more specific working memory domains.

A more recent hypothesis regarding lateralization of working memory processes states that hemispheric asymmetries are not merely domain-specific or material-specific, but instead vary on two distinct but continuous dimensions of imaginability (right hemisphere) and verbalizability [left hemisphere; Casasanto, 2003]. This hypothesis may extend to include processes that we considered here as working memory and executive functions of the basal ganglia. For instance, the current findings show left dominance in the caudate head for working-memory processes, whereas right dominance was observed for executive functions in the same region. If this hypothesis is assimilated, then in the caudate head, for example, working-memory processes may be more verbalizable, while executive function may require more imaginable processes. In line with this, we also note that executive-functioning activity was contained within the region of activity of working-memory processes in the left, but not the right, hemisphere. As it is difficult to separate working-memory and executive processes, these findings are particularly interesting because they suggest that hemispheric asymmetries may characterize these often subtle cognitive differences. The Alexander et al., [1990] model did not account for hemispheric contributions of basal ganglia structures.

Affective processes elicited a similar hemispheric asymmetry to that observed for cognitive functions. Emotion and reward processes overlapped to a greater extent in the left hemisphere, whereas in the right hemisphere, reward activities fell toward the caudate head rather than the

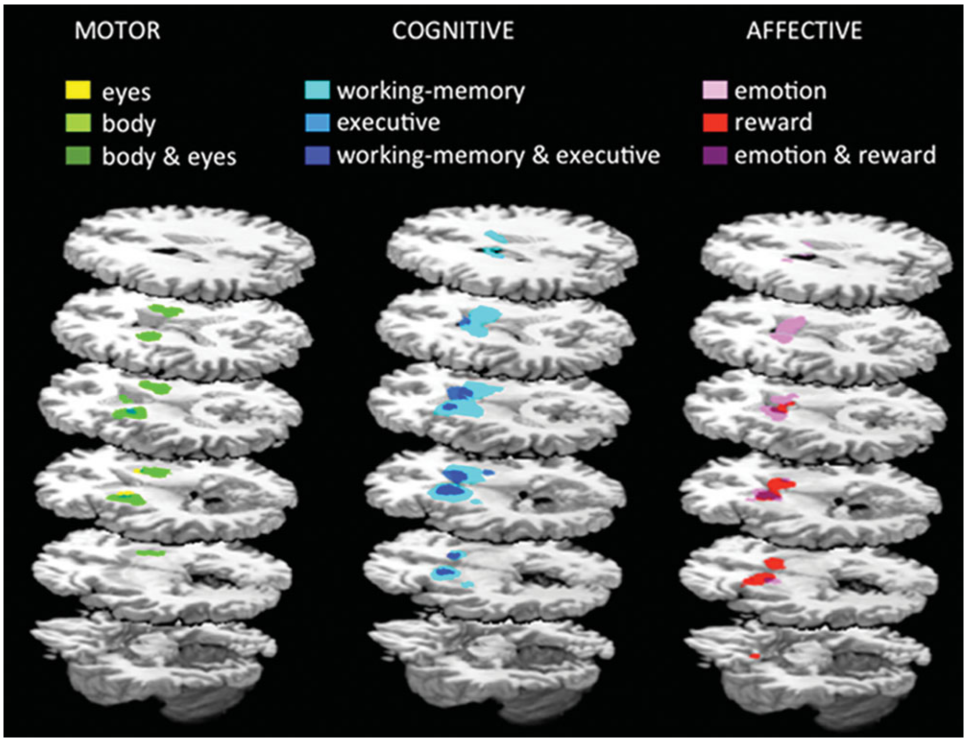

Figure 3.

Conjunction display of ALE maps showing concordance over basal ganglia nuclei for motor, cognitive, and affective functions. A voxel-wise likelihood of activation was determined using false discovery rate (FDR) $q = 0.001$ multiple comparison control. Left = Left.

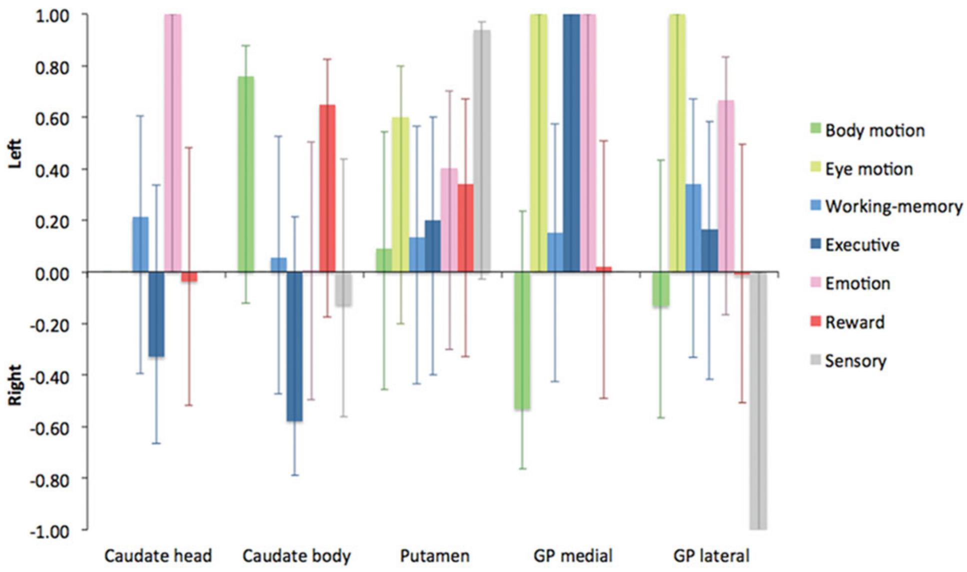

Figure 4.

Laterality indices for basal ganglia structures. Region of interest masks were applied to the thresholded ALE maps and hemispheric dominance was calculated for each region. Laterality index (LI = [Left – Right]/[Left + Right]) of >0.20 was deemed left dominance and <−0.20 right dominance, values in between were considered bilateral. Bars represent proportion of activity in each hemisphere.

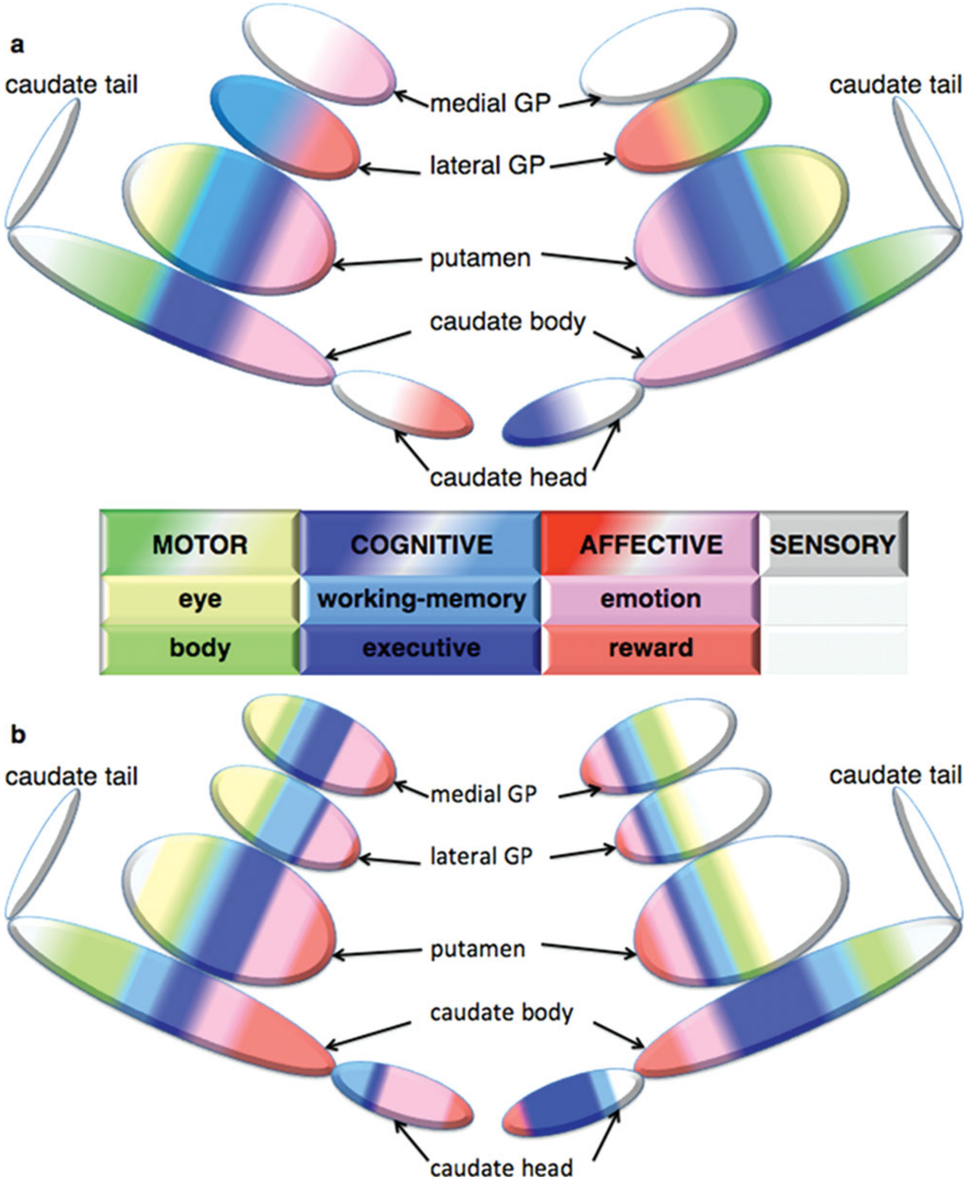

Figure 5.

Topographical model of the functions of the basal ganglia. We illustrate the basal ganglia structures in a schematic representation. Using color codes we illustrate (a) basal ganglia regions concordant across studies and (b) hemispheric dominance for each functional category; thicker stripes indicate larger hemispheric contribution. Left = Left.

caudate body. Alexander et al., [1990] did not distinguish between emotion and reward processes, but rather classified them both as a part of the limbic system. They suggested that the limbic system engaged the most ventral parts of the caudate; however, in contrast to our results, they did not consider the putamen and globus pallidus as nuclei involved in emotion and reward [Alexander et al., 1990]. Historically, emotional processing has not been ascribed to the basal ganglia and only reward processing has recently been specifically associated with the nucleus accumbens, located in the ventral striatum [Frank and Claus, 2006; Knutson and Bossaerts, 2007; Knutson and Greer, 2008; Knutson and Peterson, 2005]. Our results show key distinctions between reward and emotion processes. Specifically, our findings suggest that reward processes occupy more anterior parts of the caudate head (bilateral) and emotion processes occupy superior structures in caudate body (bilateral) and putamen (left lateralized).

Basal ganglia activation in response to somatosensory stimuli was evoked mainly by studies using noxious stimuli. Pain is a complex, multifaceted sensation that involves sensory-discriminative and affective-motivational processing, and also cognitive appraisal [Duerden and Duncan, 2009]. A recent qualitative review indicated that pain and reward pathways were processed similarly by the dorsal and ventral striatum and the globus pallidus [Leknes and Tracey, 2008]. However, the current results indicate that pain-evoked activation was largely distinct from other forms of reward and punishment, as they showed the highest concordance in the dorsal parts of the left putamen, whereas reward processes were mediated by the anterior caudate nucleus. To date, somatosensory functions are not commonly ascribed to being mediated by the basal ganglia, nor contrasted to other motor, affective or cognitive functions.

Animal studies have been key for understanding the histology [e.g., Carpenter et al., 1972; Kemp et al., 1971] and cortical connections [Haber, 2003; Bar-Gad and Bergman, 2001] of the basal ganglia. Despite the valuable contributions of animal models of basal ganglia function in relation to behavior [Chudasama, 2011], it is difficult to compare some studies to human data as tasks must be adapted for use with either population. For example, tasks used to assess cognitive abilities in animals or humans tend to be modified so that the degree of complexity can be adjusted to avoid floor or ceiling effects. Although gross similarities in brain structure and function between animals and humans exist, a major advantage of having a human model is that no assumptions need to be made to bridge the gap of performance or structural differences between species.

The nuclei of the basal ganglia are connected to brain regions implicated in motor, cognitive, affective and somatosensory functions. Several of the processes were found to overlap functionally in the nuclei of the basal ganglia that may be indicative of multimodal neuronal processing. However, some regions of the nuclei were associated with activation evoked by unique functions, a finding that could provide support for the presence of unisensory neurons in these structures.

We propose a new human model that incorporates topographical and hemispheric contributions of basal ganglia structures for motor, affective, cognitive and somatosensory functions. Basal ganglia activity is readily observed in fMRI studies of these functions (Fig. 5). In two schematic representations we illustrate (a) basal ganglia regions consistently activated across studies by using the peak likelihoods of activation for each functional category (Fig. 5a) and (b) hemispheric contributions of each nucleus of the basal ganglia for each functional category (Fig. 5b). The functional categories studied here were processed by subdivisions of the basal ganglia that were consistent with the afferent and efferent projections to and from cortical regions, which subserve these functions. For example, the head of the caudate nucleus was likely to be activated by rewarding stimuli (in the left hemisphere) and executive functioning processes (in the right hemisphere); this is likely reflective of this region's neuroanatomical connections with the orbitofrontal and medial prefrontal cortices – structures involved in these processes, respectively [Haber et al., 1995]. Additionally, somatosensation showed concordant activity in dorsolateral parts of the putamen that may reflect this region's connections to cortical areas involved in pain processing, such as the anterior cingulate cortex and insula [Mufson and Mesulam, 1982]. The basal ganglia can be considered, at least allegorically, the centre of the brain, as they are a collection of nuclei responsible for receiving and transmitting information to and from major components of the cerebral cortex that contribute to sensation, perception and behavior; fundamental activities that include motion, emotion, sensation, cognition, and reward.

The comprehensive mapping of the functions of the basal ganglia made possible by meta-analytic techniques provides valuable information that may translate into advances in clinical practices and targeted hypothesis testing. In this work, the original five-category model of the basal ganglia proposed by Alexander et al. [1990] was assessed with the inclusion of two additional categories, using functional neuroimaging data collected in healthy participants. Potentially we could have increased our categorization scheme to include such processes as motor planning, goal-directed planning, and motivation [Haber, 2003]. However, to further subcategorize the contrasts included in our seven-category model would result in a loss of statistical power. Furthermore, several of these additional cognitive processes lack unanimity in the literature to be clearly defined for meta-analytic purposes. Our classification scheme both confirms and extends previous work on the functional roles of the basal ganglia and will serve as a basis for further, more detailed analyses.

Another important consideration is that the results of this study reflect the statistical concordance across a broad range of studies classified into categories that included an array of contrasts. The contrast selection was based on thoroughly researched predefined criteria. However, the classification of functions is inherently difficult as some higher order tasks may recruit several processes and as a result, this could account for some of the observed overlap. Optimally, data of identical contrasts should be analyzed, as they would be less influenced by methodological factors; however, such an approach would allow the inclusion of fewer neuroimaging studies and would make meta-analytic analyses difficult to interpret. An additional consideration is that methodological approaches selected by the original sources also varied, such as imaging parameters and statistical approaches. Nonetheless, we did take steps to control for aspects of the methodological variance, such as choosing only fMRI studies and selecting articles that performed whole-brain analyses.

An additional point of interest that could not be assessed with these data is the issue of age-related functional differences in the basal ganglia. More subtle categorizations of function or age-range selections could not be completed as it would significantly reduce the power of the analyses. Despite these limitations, it is encouraging that we observed convergence of evidence over a large series of data, compiled over independent research groups studying common domains (i.e., motor, cognition, affect, and somatosensation).

In summary, basal ganglia structures are involved not only in motor processes but also cognitive, affective, and somatosensory functions key to a host of human behaviors. Our analyses provide functional distinctions of basal ganglia structures, as well as lateralization information, an aspect that was previously neglected. This work can serve as a basis for understanding subcortical/cortical interactions and future work could focus on more specific functions of the basal ganglia. Also, the proposed normative adult model could be used for *a prori* region-of-interest analyses to assess basal ganglia development or examine dysfunction in relation to neuropsychiatric disease.

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