## Contents

1	Introduction: the issues					
	1.1	Introd	luction	1		
	1.2	Rewards and punishers				
	1.3	The a	pproaches taken to emotion and motivation	5		
	1.4	The p	lan of the book	7		
2	The	nature	e of emotion	10		
	2.1	Introd	luction	10		
	2.2	A the	ory of emotion	11		
	2.3	Different emotions				
	2.4	Refinements of the theory of emotion				
	2.5	The c	lassification of emotion '	25		
	2.6	Other	theories of emotion	26		
		2.6.1	The James-Lange and other bodily theories	26		
		2.6.2	Appraisal theory	30		
		2.6.3	Dimensional and categorical theories of emotion	31		
		2.6.4	Other approaches to emotion	31		
	2.7	Indivi	dual differences in emotion, personality, and emotional			
		intellig	gence	32		
	2.8	Cogni	ition and Emotion	35		
	2.9	Emotion, motivation, reward, and mood				
	2.10	2.10 The concept of emotion				
	2.11	2.11 Advantages of the approach to emotion described here				
		(Rolls	' theory of emotion)	38		
3	The	functio	ons of emotion:			
rev	vard,	punisł	nment, and emotion in brain design	41		
	3.1	Introd	luction	41		
	3.2	Brain	design and the functions of emotion	43		
		3.2.1	Taxes, rewards, and punishers: gene-specified goals			
			for actions, and the flexibility of actions	43		
		3.2.2	Explicit systems, language, and reinforcement	47		
		3.2.3	Special-purpose design by an external agent vs evo-			
			lution by natural selection	48		
	3.3	Selec	tion of behaviour: cost-benefit 'analysis'	49		

	3.4	Further functions of emotion	51
		3.4.1 Autonomic and endocrine responses	51
		3.4.2 Flexibility of behavioural responses	52
		3.4.3 Emotional states are motivating	53
		3.4.4 Communication	54
		3.4.5 Social attachment	57
		3.4.6 Separate functions for each different primary rein-	
		forcer	57
		3.4.7 The mood state can influence the cognitive evalua-	
		tion of moods or memories	58
		3.4.8 Facilitation of memory storage	58
		3.4.9 Emotional and mood states are persistent, and help	)
		to produce persistent motivation	59
		3.4.10 Emotions may trigger memory recall and influence	
		cognitive processing	59
	3.5	The functions of emotion in an evolutionary, Darwinian, con-	
		text	59
	3.6	The functions of motivation in an evolutionary, Darwinian,	
		context	61
	3.7	Are all goals for action gene-specified?	62
4	The	brain mechanisms underlying emotion	63
	4.1	Introduction	63
	4.2	Overview	63
	4.3	Representations of primary reinforcers	66
		4.3.1 Taste	67
		4.3.2 Smell	67
		4.3.3 Pleasant and painful touch	67
		4.3.4 Visual stimuli	69
	4.4	Representing potential secondary reinforcers	71
		4.4.1 The requirements of the representation	71
		4.4.2 High capacity	74
		4.4.3 Objects, and not their reward and punishment as-	
		sociations, are represented in the inferior temporal	
		visual cortex	75
		4.4.4 Object representations	77
		4.4.5 Invariant representations of faces and objects in the	
		inferior temporal visual cortex	78
		4.4.6 Face expression, gesture and view represented in a	
		population of neurons in the cortex in the superior	

		temporal sulcus	89
	4.4.7	The brain mechanisms that build the appropriate	
		view-invariant representations of objects required for	
		learning emotional responses to objects, including	
		faces	89
4.5	The c	rbitofrontal cortex	91
	4.5.1	Historical background	91
	4.5.2	Topology	92
	4.5.3	Connections	93
	4.5.4	Effects of damage to the orbitofrontal cortex	95
	4.5.5	Neurophysiology and functional neuroimaging of the	
		orbitofrontal cortex	97
	4.5.6	The human orbitofrontal cortex	131
	4.5.7	A neurophysiological and computational basis for	
		stimulus-reinforcer association learning and rever-	
		sal in the orbitofrontal cortex	140
	4.5.8	Executive functions of the Orbitofrontal cortex	147
4.6	The a	Imygdala	149
	4.6.1	Associative processes involved in emotion-related	
		learning	149
	4.6.2	Connections of the amygdala	155
	4.6.3	Effects of amygdala lesions	157
	4.6.4	Neuronal activity in the primate amygdala to reinforc-	
		ing stimuli	164
	4.6.5	Responses of these amygdala neurons to novel stim-	
		uli that are reinforcing	170
	4.6.6	Neuronal responses in the amygdala to faces	172
	4.6.7	Evidence from humans	175
	4.6.8	Amygdala summary	178
4.7	The c	ingulate cortex	179
		Perigenual cingulate cortex and affect	181
	4.7.2	Mid-cingulate cortex, the cingulate motor area, and	
		action-outcome learning	185
4.8	Huma	an brain imaging investigations of mood and depres-	
	sion		187
4.9	Outpu	it pathways for emotional responses	188
		The autonomic and endocrine systems	188
	4.9.2	Motor systems for implicit responses, including the	
		basal ganglia	189

		4.9.3	Output systems for explicit responses to emotional		
			stimuli	190	
		4.9.4	Basal forebrain and hypothalamus	191	
		4.9.5	Basal forebrain cholinergic neurons	191	
		4.9.6	Noradrenergic neurons	194	
	4.10	Effect	s of emotion on cognitive processing and memory	194	
	4.11	Latera	ality effects in human emotional processing	200	
	4.12	Sumn	nary	202	
	4.13	Colou	ir plates	205	
5	Hun	ger		221	
	5.1	Introd	luction	221	
	5.2	Peripl	heral signals for hunger and satiety	221	
	5.3	The c	control signals for hunger and satiety	224	
		5.3.1	Sensory-specific satiety	224	
		5.3.2	Gastric distension	230	
		5.3.3	Duodenal chemosensors	230	
		5.3.4	Glucostatic hypothesis	230	
		5.3.5	Body fat regulation - leptin or OB protein	231	
		5.3.6	Conditioned appetite and satiety	232	
	5.4	The b	prain control of eating and reward	233	
		5.4.1	The hypothalamus	233	
		5.4.2	Brain mechanisms for the reward produced by the		
			taste of food	243	
		5.4.3	Convergence between taste and olfactory process-		
			ing to represent flavour	253	
		5.4.4	Brain mechanisms for the reward produced by the		
			odour of food	254	
		5.4.5	The responses of orbitofrontal cortex taste and olfac-		
			tory neurons to the sight of food	259	
		5.4.6	Functions of the amygdala and temporal cortex in		
			feeding	259	
		5.4.7	Functions of the orbitofrontal cortex in feeding	263	
		5.4.8	Functions of the striatum in feeding	266	
	5.5	5.5 Obesity, bulimia, and anorexia		271	
	5.6	Concl	lusions on reward, affective responses to food, and the		
		contro	ol of appetite	273	
6	Thirst				
	6.1	Introd	luction	274	
	6.2	2 Cellular stimuli for drinking			

	6.3	Extracellu	ular thirst stimuli	276
		6.3.1 Ex	tracellular stimuli for thirst	276
		6.3.2 Ro	ble of the kidney in extracellular thirst: the renin-	
		ar	giotensin system	278
		6.3.3 Ca	ardiac receptors for thirst	279
	6.4	Control c	f normal drinking	279
	6.5	Reward a	and satiety signals for drinking	282
	6.6	Summary	/	286
7	Bra	n-stimula	tion reward	288
	7.1	Introducti	on	288
	7.2	The natu	re of the reward produced	288
	7.3	The locat	ion of brain-stimulation reward sites in the brain	292
	7.4	The effect	ts of brain lesions on intracranial self-stimulation	293
	7.5	The neur	ophysiology of reward	294
		7.5.1 La	teral hypothalamus and substantia innominata	294
		7.5.2 Or	bitofrontal cortex	296
		7.5.3 Ar	nygdala	298
		7.5.4 Nu	ucleus accumbens	299
		7.5.5 Ce	entral gray of the midbrain	299
	7.6	Some of	the properties of brain-stimulation reward	300
			ck of satiety with brain-stimulation reward	300
		7.6.2 Ra	apid extinction	302
		7.6.3 Pr	iming	302
	7.7	Stimulus	bound motivational behaviour	304
	7.8	Conclusio	ons	305
	7.9	Apostasis	3	306
8	Pha	rmacolog	y of emotion, reward, and addiction; the basal	
ga	nglia			308
	8.1	Introduct	on	308
	8.2		drenergic hypothesis	311
	8.3		e and reward	312
			ppamine and electrical self-stimulation of the brain	312
		8.3.2 Se	elf-administration of dopaminergic substances, and	
		ac	ldiction	314
			haviours associated with the release of dopamine	316
		8.3.4 Th	e activity of dopaminergic neurons and reward	318
	8.4	The base	I ganglia	321
		8.4.1 Sy	stems-level architecture of the basal ganglia	322
		8.4.2 Ef	fects of basal ganglia damage	323

		8.4.3	Neuronal activity in the striatum	325
		8.4.4	What computations are performed by the basal gan-	
			glia?	339
		8.4.5	How do the basal ganglia perform their computa-	
			tions?	340
		8.4.6	Synthesis on the role of dopamine in reward and ad-	
			diction	348
		8.4.7	Synthesis: emotion, dopamine, reward, punishment,	
			and action selection in the basal ganglia	350
	8.5	Opiate	e reward systems, analgesia, and food reward	352
	8.6	Pharn	nacology of depression in relation to brain systems	
		involv	ed in emotion	353
	8.7	Pharn	nacology of anxiety in relation to brain systems in-	
		volved	d in emotion	354
	8.8	Canna	abinoids	355
	8.9	Overv	iew of behavioural selection and output systems in-	
		volved	d in emotion	355
9	Sex	ual bel	haviour, reward, and brain function; sexual selec-	
		pehavio		358
	9.1		luction	358
	9.2		selection, attractiveness, and love	360
	•		Female preferences	361
			Male preferences	363
			Pair-bonding, and Love	366
	9.3		ata attachment, care, and parent-offspring conflict	367
	9.4	Sperm competition and its consequences for sexual be-		
		havio		368
	9.5	Conce	ealed ovulation and its consequences for sexual be-	
		havio	ur	375
	9.6	Sexua	al selection of sexual and non-sexual behaviour	376
		9.6.1	Sexual selection and natural selection	376
		9.6.2	Non-sexual characteristics may be sexually selected	
			for courtship	379
	9.7	Indivi	dual differences in sexual rewards	381
		9.7.1	Overview	381
		9.7.2	How might different types of behaviour be produced	
			by natural selection altering the relative reward value	
			of different stimuli in different individuals?	384
		9.7.3	How being tuned to different types of reward could	

	help to produce individual differences in sexual be- haviour	386
	9.8 The neural reward mechanisms that might mediate some	500
	aspects of sexual behaviour	387
	9.9 Neural basis of sexual behaviour	395
	9.10 Conclusion	398
10	Emotional feelings and consciousness: a theory of con-	
sci	Dusness	400
	10.1 Introduction	400
	10.2 A theory of consciousness	401
	10.3 Dual routes to action	411
	10.4 Content and meaning in representations	418
	10.5 Discussion	420
	10.6 Conclusions and comparisons	423
11	Conclusions, and broader issues	426
	11.1 Conclusions	426
	11.2 Decision-making	431
	11.2.1 Selection of mainly autonomic responses, and their	
	classical conditioning	431
	11.2.2 Selection of approach or withdrawal, and their clas-	
	sical conditioning	431
	11.2.3 Selection of fixed stimulus-response habits	432
	11.2.4 Selection of arbitrary behaviours to obtain goals,	100
	action-outcome learning, and emotional learning	432
	11.2.5 The roles of the prefrontal cortex in decision-making	400
	and attention	433 440
	11.2.6 Neuroeconomics, reward value, and expected utility 11.2.7 Selection of actions by explicit rational thought	440 444
	11.3 Emotion and ethics	444
	11.4 Emotion and literature	449
	11.5 Close	452
А	Neural networks and emotion-related learning	454
	A.1 Neurons in the brain, the representation of information, and	
	neuronal learning mechanisms	454
	A. 1.1 Introduction	454
	A.1.2 Neurons in the brain, and their representation in neu-	
	ronal networks	454

		A.1.3	A formalism for approaching the operation of single			
			neurons in a network	456		
		A. 1.4	Synaptic modification	458		
		A.1.5	Long-Term Potentiation and Long-Term Depression	459		
		A. 1.6	Distributed representations	464		
	A.2	Patter	rn association memory	466		
		A.2.1	Architecture and operation	466		
		A.2.2	A simple model	469		
		A.2.3	The vector interpretation	472		
		A.2.4	Properties	472		
		A.2.5	Prototype extraction, extraction of central tendency,			
			and noise reduction	475		
		A.2.6	Speed	475		
		A.2.7	Local learning rule	476		
		A.2.8	Implications of different types of coding for storage			
			in pattern associators	482		
	A.3	Autoa	association memory: attractor networks	483		
		A.3.1	Architecture and operation	483		
		A.3.2	Introduction to the analysis of the operation of au-			
			toassociation networks	485		
		A.3.3	Properties	486		
	A.4	Coup	led attractor networks	491		
	A.5	Reinfo	prcement learning	493		
		A.5.1	Associative reward-penalty algorithm of Barto and			
			Sutton	494		
		A.5.2	Error correction or delta rule learning, and classical			
			conditioning	496		
		A.5.3	Temporal Difference (TD) learning	497		
В	Rev	Reward reversal in the orbitofrontal cortex - a model				
	B.1					
	B.2	The n	nodel of stimulus-reinforcer association reversal	503		
		B.2.1	The network	504		
		B.2.2	Reward reversal: the operation of the rule module			
			neurons	507		
		B.2.3	The neurons in the model	509		
		B.2.4	The synapses in the model	510		
	B.3		ation of the reward reversal model	511		
	B.4	A mo	del of reversal of a conditional object-response task			
			e dorsolateral prefrontal cortex	515		

	B.5	Evaluation of the models	517
	B.6	Integrate-and-Fire model equations and parameters	521
	B.7	Simulation of fMRI signals: haemodynamic convolution of	
		synaptic activity	522
С	Glos	ssary	525
Re	ferend	ces	528
Index			602