

Emotions and feelings

- sadness, fear, anger verbal expression of different states

Emotional states

- are observable directly in facial expressions or other overt behaviours, indirectly with psychophysiological tests and endocrine assays

Early theories about emotional brain

Rethinking the Emotional Brain

Joseph LeDoux^{1,2,*}

¹Center for Neural Science and Department of Psychology, New York University, New York, NY 10003 USA

²Emotional Brain Institute, New York University and Nathan Kline Institute, Orangeburg, NY 10962 USA

*Correspondence: jel1@nyu.edu

DOI 10.1016/j.neuron.2012.02.004

I propose a reconceptualization of key phenomena important in the study of emotion—those phenomena that reflect functions and circuits related to survival, and that are shared by humans and other animals. The approach shifts the focus from questions about whether emotions that humans consciously feel are also present in other animals, and toward questions about the extent to which circuits and corresponding functions that are present in other animals (survival circuits and functions) are also present in humans. Survival circuit functions are not causally related to emotional feelings but obviously contribute to these, at least indirectly. The survival circuit concept integrates ideas about emotion, motivation, reinforcement, and arousal in the effort to understand how organisms survive and thrive by detecting and responding to challenges and opportunities in daily life.

Survival circuits

- defence, energy/nutrition maintenance, fluid balance, thermoregulation, procreation
- each circuit is tuned to certain classes of environmental and/or internal physiological state stimuli → different triggers

Survival circuits

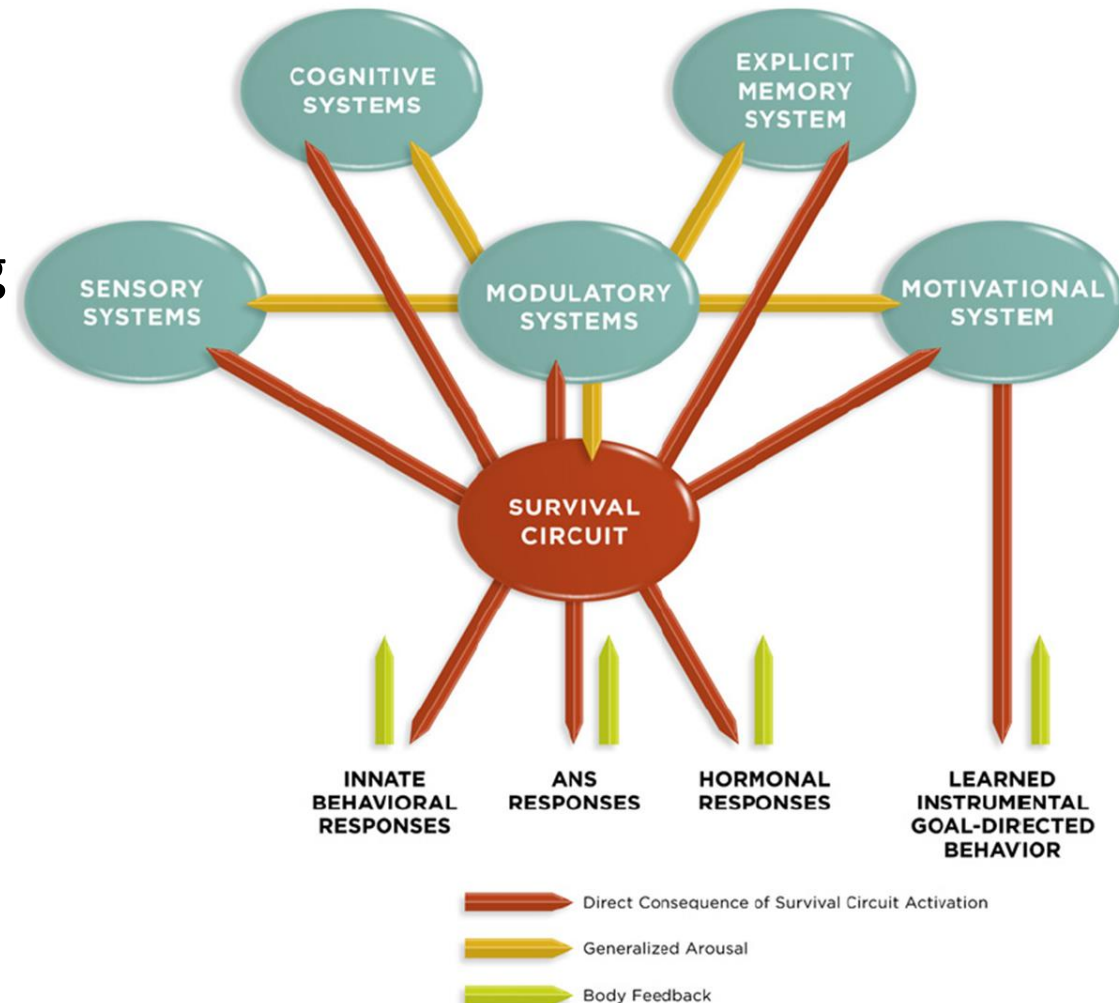
- networks evaluate stimulus value on the basis of innate programming or by the way of past experience that leads to the formation of associations between innately significant events and novel stimuli

Outward responses of survival circuits

- can vary between species → escape: swimming, flying, running

Consequences of survival circuits activation

- behavioural, autonomic and endocrine responses
- increase of arousal
- motivational systems
- working memory
- early sensory processing



Emotions

- **set of physiological responses:**
 - in the brain - changes in arousal level and in cognitive functions such as attention, memory processing, and decision strategy
 - in the body proper – endocrine, autonomic and musculoskeletal responses
- basic, complex, social emotions

Emotions

- automatic, largely unconscious responses
- triggered when the brain detects a positively or negatively charged significant stimulus

Stimuli

- trigger emotions automatically even in the absence of experience (= are said to have emotional competence)
- some otherwise insignificant objects and events can acquire emotional significance through associative learning with emotionally competent stimuli
- can trigger physiological responses **in the absence of consciousness and feelings**

Emotional reactions

- conserved throughout the evolution of species
- determine significant stimuli in everyday life
- influence early stages of sensory information analysis

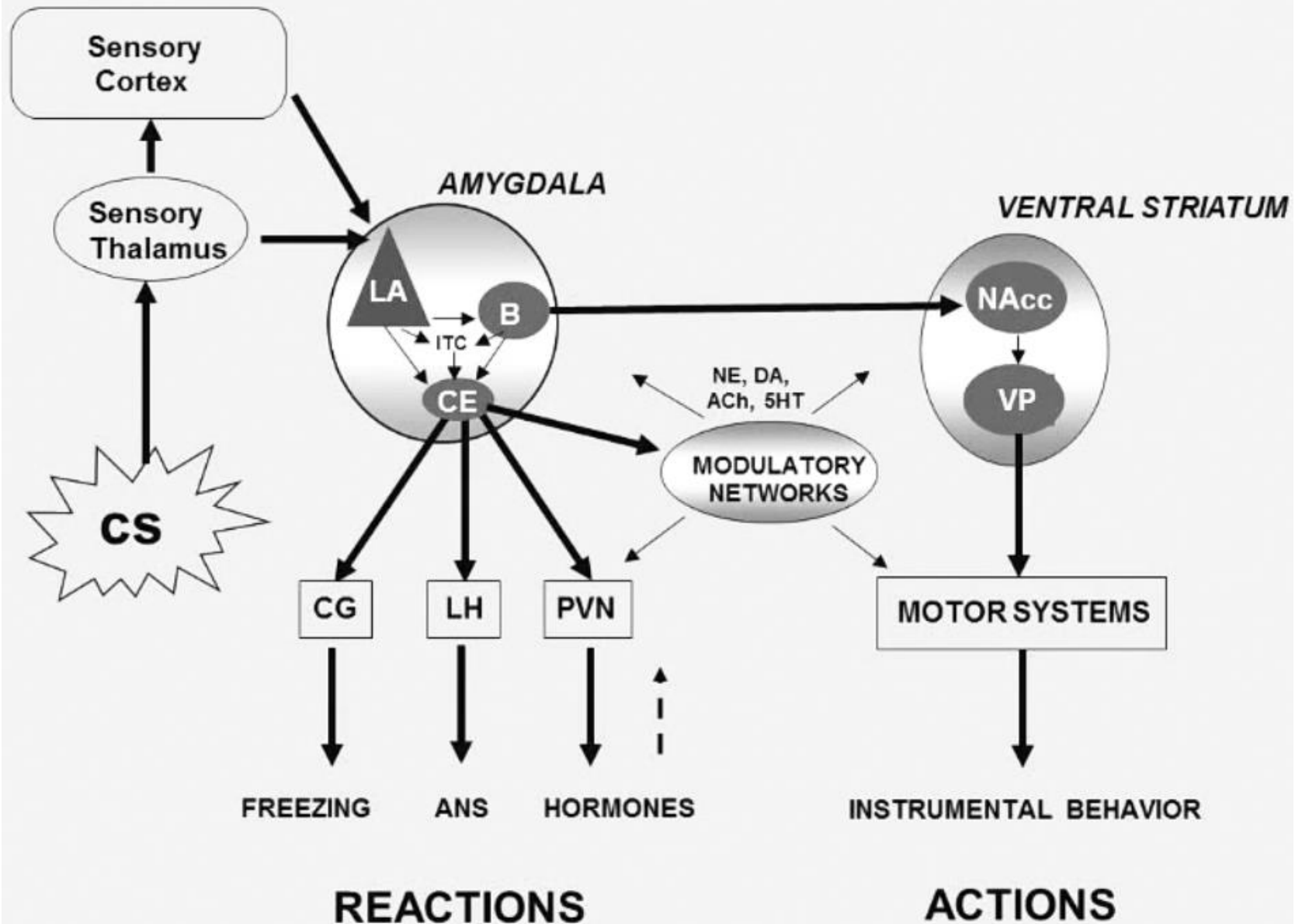
Summary of some features of some emotion systems

- contribute to survival
- engage the whole organism
- synchronize brain resources
- inhibit non-relevant brain functions
- potentiate relevant motivational systems

Amygdala

Defense conditioning

CIRCUITS MEDIATING THREAT-ELICITED REACTIONS AND THREAT-MOTIVATED ACTIONS



Amygdala in humans

- activity increases in CS-US pairing
- fearful facial expression also activate the amygdala, even when presented subliminally
- activated also with positive stimuli – food, sex, money

Amygdala - lesions

- impair defence conditioning
- impair recognition of fearful facial expression

Structures of the limbic system

- cingulate and parahippocampal gyri, hippocampal formation (hippocampus, dentate gyrus, subiculum)
- hypothalamus, mammillary bodies, septum, nucleus accumbens, amygdala, periaqueductal grey
- orbitofrontal cortex

Learning and memory

- amygdala – implicate
- hippocampus – explicit

The role of context

- animal learns to increase its contact with environments in which it has previously encountered stimuli essential for survival and to minimize contact with environments that are aversive or dangerous (involves information about place, a process that requires the hippocampus)

Feelings

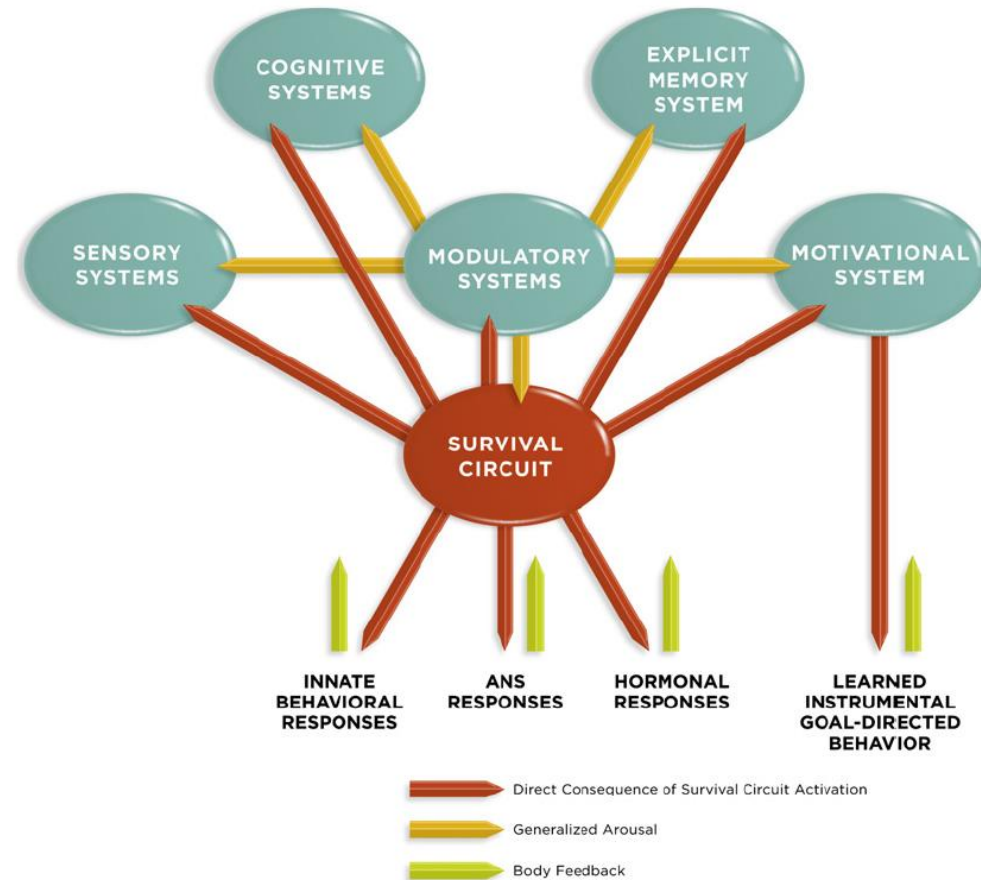
- the conscious experience of somatic and cognitive changes
 - consciousness
 - language – verbal expressions
- insular cortex, secondary somatosensory cortex, cingulate cortex, hypothalamus, upper brain stem
- facilitate learning about objects and situations that cause emotional responses
- increase adaptability in responding to dangerous or advantageous situations

Damage to some sectors of prefrontal cortex

→ impaired social emotions and related feelings, sociopathic personalities: unable to hold jobs, cannot maintain stable social relationships and financial independence, are prone to violate social conventions

Motivational states

- processes mediating the goal-directed responses to changes of internal and external environment
- part of survival circuits



Motivational states influence

- attentiveness
- goal selection
- investment of effort in the pursuit of goals
- responsiveness to stimuli

Motivational states

- interaction of internal (physiological error signals and the circadian clock) and external inputs (incentive stimuli)
- positive feedback between incentive stimuli and motivational states helps ensure that complex behavioural sequences are completed
- levels:
 - alterations in internal physical conditions (drives - hunger, thirst, temperature ...)
 - personal or social aspirations acquired by experience

Dopamin – reward-prediction error signal

- dopamin – reward-prediction error signal, facilitates the mechanisms of learning and memory (declarative and associative)

„Reward system“

- may provide a common logic for goal selection

medial forebrain bundle (dopaminergic) – ventral tegmentum and
ncl. accumbens

Motivational states

- steer behaviour toward specific positive goals and away from negative ones
- attainment of the goal ↓ intensity of the drive state – motivation behaviour ceases
- ↑ general alertness energizing the individual to act

Addiction

- psychological dependence X physical dependence (greatest in opiate addiction)
- tolerance

Addictive drugs

- activate reward circuitry
- mechanisms:
 - dopamin-dependent - ↑ extracellular concentration of dopamin in ncl.accumbens
 - dopamin-independent - opioid receptors

Reticular formation (RF)

- the core of the brain stem
- populations of neurons with specific functions:
 - pattern generator neurons
 - modulatory function

Pattern generators

- groups of neurons near the cranial motor nuclei (e.g. n. vagus, n. trigeminus, n. facialis, ...)
- control reflexes (e.g. vestibuloocular, corneal reflex, gag reflex, coughing) and simple stereotypic behaviour (e.g. chewing, swallowing, vomiting ...)
- a complex pattern generator - breathing
- emotional facial expressions

Modulatory systems

- localized groups of neurons with long ascending and descending axons
- monoaminergic (noradrenalin, serotonin, dopamine, histamine) a cholinergic (acetylcholine)

Ascending system - arousal and consciousness

= ascending arousal system

- from monoaminergic cell groups in midbrain: raphe ncl. - **serotonin**, locus ceruleus – **noradrenalin** and tuberomamillary ncl.– **histamine**
- from pedunculo pontine and laterodorsal tegmental nuclei - **acetylcholine**
- parabrachial ncl. – **glutamate**
- lateral hypothalamus – **orexin**
-

Ascending arousal system

- diffuse cortical projections:
 - via thalamus (relay and intralaminar nuclei)
 - via lateral hypothalamic area and basal forebrain cell groups
- lesions that disrupt either of these two branches impair consciousness

Ascending arousal system

- increase wakefulness and vigilance, as well as the responsiveness of cortical and thalamic neurons to sensory stimuli = **arousal**
- **consciousness** - property of being awake, of being aware of oneself and one`s place in the environment
- modulation of circadian rhythms (sleep-wake cycle)

Ascending projections – cognitive performance

- noradrenalin (locus ceruleus) – attention
- dopamine – reward-based learning
- monoaminergic inputs to dorsolateral prefrontal cortex improve working memory

Modulation of pain

- from raphe magnus nucleus (serotonin)
- from locus ceruleus (noradrenalin)
- periaqueductal grey matter (enkephalins) project to raphe magnus nucleus
- agonists to 5-HT_{1D} receptors or monoamine reuptake blockers (e.g. SSRI) – pain treatment

Modulation of motor activity

- dopamine (substantia nigra → basal ganglia)
- drugs activating serotonin receptors can induce hyperactivity, myoclonus, tremor („serotonin syndrome“)
- noradrenergic neurons – projections to motor neurons → facilitation of excitatory inputs
- note: increased beta-adrenergic activation during defence reaction can exaggerate motor responses and produce tremor

Pathology in modulatory systems

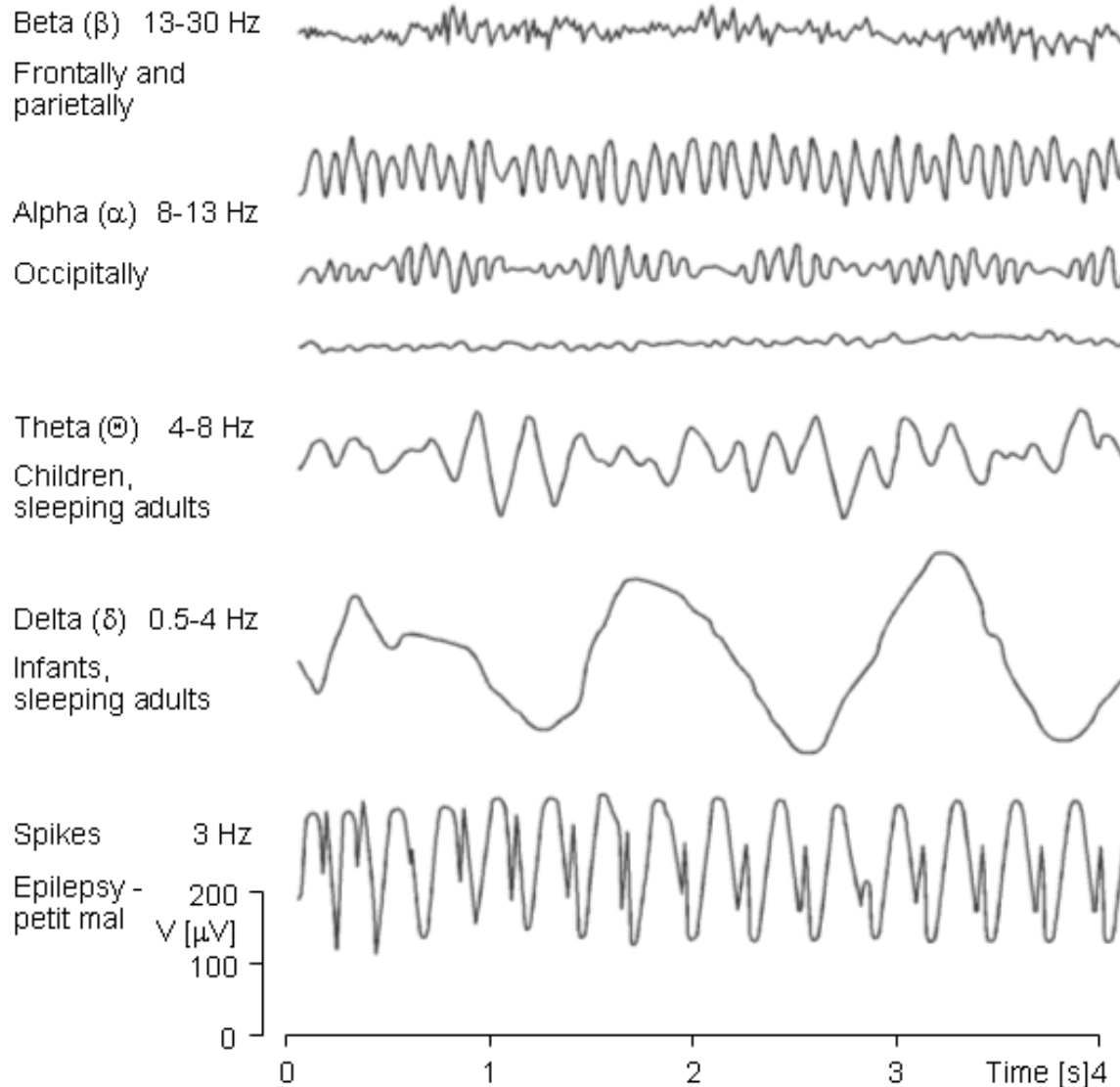
- Alzheimer`s disease – acetylcholine
- schizophrenia – dopamine
- depression – serotonin a noradrenalin

Electroencephalography - recording

- monopolar arrangement:
 - active electrode
 - indifferent electrode

= referential recording
- bipolar recording
- lead (channel)
- ground electrode
- voltage in microvolts
- international system 10-20
- eeg cap

Electroencephalography



Sleep

- actively induced and highly organized brain state with different phases
- criteria: reduced motor activity; decreased response to stimulation; stereotypic posture (lying down with eyes closed); relatively easy reversibility (in contrast to coma)

Non-REM sleep

- **slow-wave sleep**
- ↓ sympathetic outflow,
↓HR, ↓ BP
- skeletal muscle relaxed,
muscle tone and reflexes
are intact
- ↑ threshold for arousal
by sensory stimuli

REM sleep

- **rapid eye movements**
- EEG patterns of REM sleep and wakefulness are similar (paradoxical sleep)
- atonia - ↓ skeletal muscle tone (except eye muscle and diaphragm)

Sleep

- non-REM and REM stages = 90-110 minutes
- 4-6 times per night
- non-REM 3 and 4 stages duration decrease
REM stages duration increase

Sleep period change over the life span

REM sleep

- in the newborn REM phases constitute about 50 % of sleep and the proportion declines rapidly until about 4 years of age

Sleep

- in young adults:
 - 50-60 % non-REM stage 2 sleep
 - 20-25 % REM sleep
 - 15-20 % non-REM stages 3 and 4 sleep
 - 5 % non-REM stage 1 sleep
- Stage 3 and 4 are now recognized as a stage 3

Sleep and dreams

- in both REM and non-REM stages
- reports of non-REM dreams tend to be shorter, less visual, less emotional, and more conceptual and usually related to the current life of the dreamer
- REM dreams tend to be relatively long, primary visual, somewhat emotional, and usually not connected to the immediate events of the everyday life of the dreamer

Endogenous circadian rhythms

Ncl. suprachiasmaticus = „master clock“

Sleep and melatonin

Sleepiness

Sleep regulation

Sleep disorders

- Insomnia - inability to sleep for a sufficient length of time to produce a subjective sense of refreshment
 - stress, jet lag, coffee, working night shifts
 - associated with depression
- Sleep apnea - pattern of interrupted breathing during sleep causing waking up dozens or more times with the results - no slow-wave sleep and less time in REM sleep

Sleep disorders

- Narcolepsy - REM sleep attacks during the day without going through non-REM sleep
 - 30 seconds - 30 minutes
 - the onset of sleep can be abrupt – cataplexy
 - ↓↓ orexin (=hypocretin)

Cerebral cortex

- thickness 2-(4)5 mm
- surface - 250 000 mm²
- pyramidal and granule cells

Cerebral cortex

- pyramidal neurons: projection, association, commissural
 - glutamate
- granule neurons: local interneurons
 - glutamate and GABA

Cerebral cortex

- isocortex = neocortex
- allocortex =
archicortex (hippocampus, gyrus
dentatus, gyrus fasciolaris, gyrus
parahippocampalis)
+ paleocortex (olfactory area)

Fluid balance

- motivational state: thirst
- primary drinking: response to an error signal
- secondary drinking: to avoid severe dehydration
- motivational system anticipate the appearance and disappearance of error signals - termination of drinking before plasma osmolality is restored

- volume and osmolality
- endocrine (kidney – RAAS) and neural sensors (baroreceptors, osmoreceptors v SFO a OVLT)
- integration in hypothalamus – PVN – vasopresin

Feeding behaviour

- feedback control system - body weight seems to be regulated by a set point
- the apparent set point of an individual can vary with stress, palatability of the food, exercise, and many other environmental and genetic factors → a control system that has no formal set-point mechanism but which nevertheless functions as if there were a set point
- long-term signals - leptin, insulin
- short-term signals - ghrelin, cholecystokinin

Feeding behaviour in animals

- experimental stimulation of the ncl. paraventricularis suppresses feeding (lesions produce overeating and severe obesity)
- experimental stimulation of the lateral hypothalamus elicits feeding (lesions produce severe neglect of eating)

Feeding behaviour

- ventromedial and lateral hypothalamus **are not satiety and feeding centers**, rather neural circuits mediating homeostatic functions such as feeding are distributed among several structures in the brain

Temperature regulation

- feedback detectors – peripheral (throughout the body) and central (anterior hypothalamus)

Temperature regulation

- hypothalamus integrates peripheral and central information relevant to temperature regulation
- warm-sensitive neurons, cold-sensitive neurons

Temperature regulation

Experimental stimulation of:

- anterior hypothalamus: ↑ heat dissipation - dilation of blood vessels in the skin, panting, suppression of shivering → decrease body temperature
- posterior hypothalamus : ↑ heat conservation → increase body temperature

Temperature regulation

- long-term control of endocrine responses to temperature challenges (thyroxin)

Temperature regulation

- in addition to driving appropriate autonomic, endocrine, and nonvoluntary skeletal responses, the error signal of the temperature control system can also drive voluntary behaviors that minimize the error signal

Temperature regulation

set point: 37 °C; varies diurnally, decreasing to a minimum during sleep

- can be altered by the action of pyrogens during illness (macrophage product interleukin-1) in the preoptic area - increase the set point.

stimulation of the antipyretic area (septal nuclei anterior to the preoptic area) limits the magnitude of the fever (vasopressin as transmitter)

Hypothalamus

- coordinates the peripheral expression of emotional states
- electrical stimulation can evoke various (from simple to more complex) autonomic and somatic responses characteristic for specific emotional states

Hypothalamus

- it is a structure that integrates various inputs to ensure a well-organized, coherent, and appropriate set of autonomic, endocrine and behavioural responses

Hypothalamus

- Blood pressure and electrolyte composition.
- Energy metabolism.
- Reproductive (sexual and parental) behaviors.
- Body temperature.
- Defensive behavior.
- Sleep-wake cycle.