Neuroeconomics:
Noise in the brain, impulsiveness, and economic decision-making

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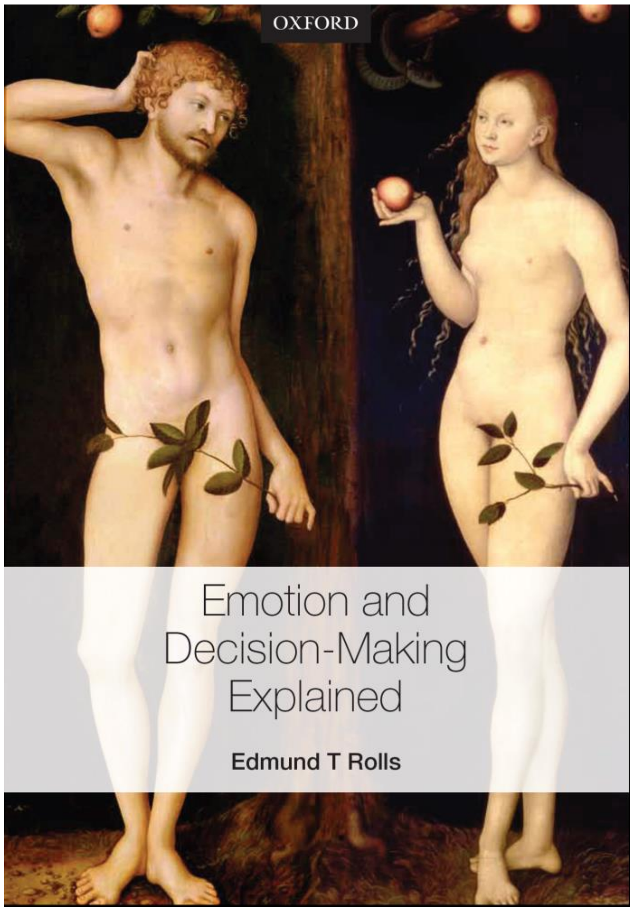


Oxford University Press 2014

Neuroimaging:
F. Grabenhorst
C. McCabe
I. Araujo
W. Cheng
J. Feng

Neuropsychology:
J. Hornak
H. Berlin

Orbitofrontal Neurophysiology:
J.V. Verhagen
M. Kadohisa
H. Critchley

Computational Neuroscience
S.M. Stringer
G. Deco (Barcelona)
A. Treves (SISSA, Trieste)
P. Mills
T. Webb (Warwick)
L. Robinson (Warwick)

Inferior Temporal Neurophysiology
N. Aggelopoulos

Hippocampal Neurophysiology
J.-Z. Xiang

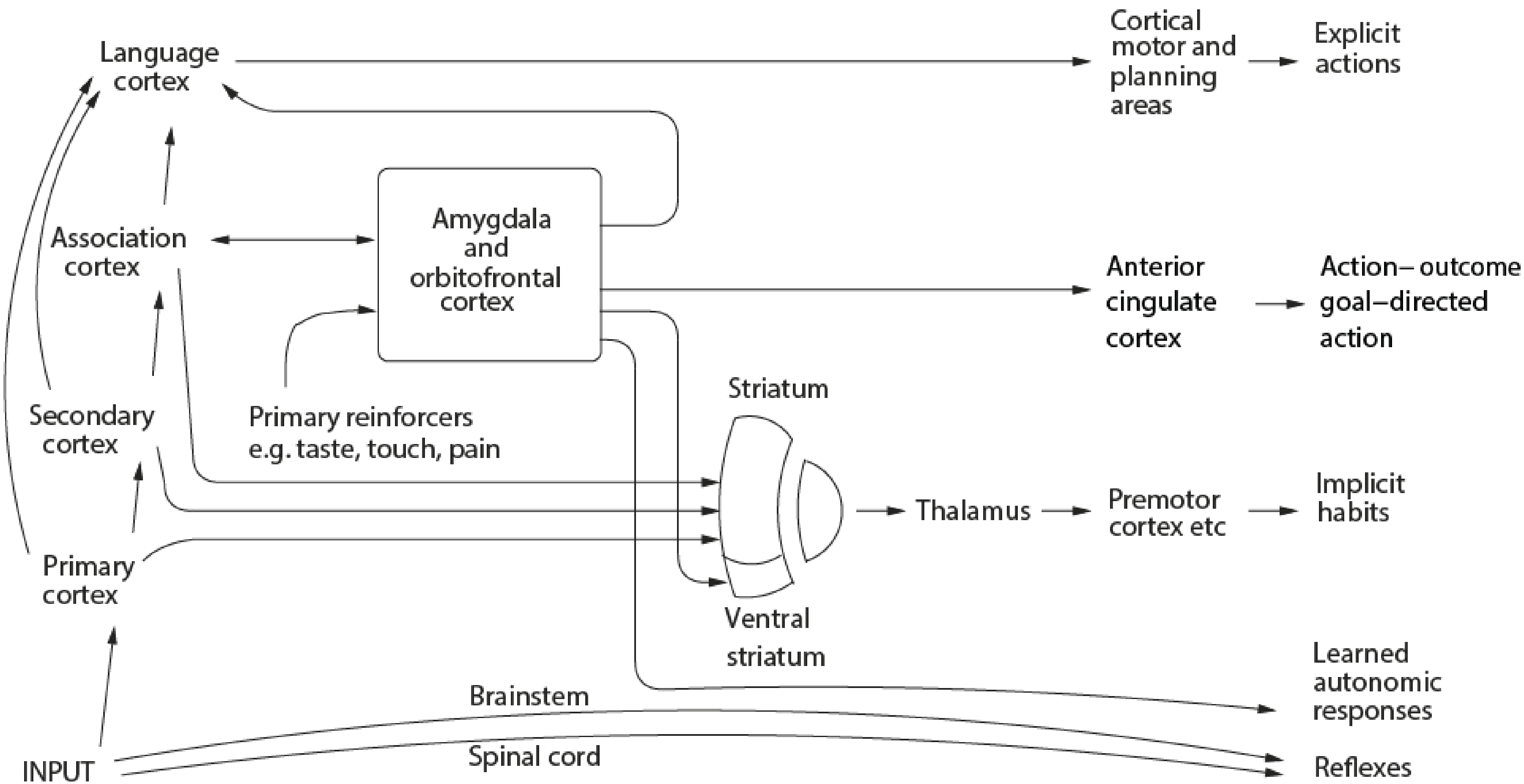
Emotion: States elicited by Instrumental Reinforcers.

Role of Rewards & Punishers in Brain Design.

- Reward - an arbitrary instrumental action is performed to obtain a reward
- Punisher - an arbitrary instrumental action is performed to escape from or avoid a punisher
- Via natural selection, genes have built receptors for stimuli that by helping to encode primary (unlearned) rewards and punishers increase fitness.
- These gene-specified rewards and punishers (reinforcers) provide the goals for actions, which can be arbitrary, flexible and learned.
- Emotions are the states elicited by these gene-specified primary reinforcers and by secondary (learned) rewards and punishers. (Pleasures)
- Emotions are thus states elicited by rewards and punishers, which are the goals for action: emotions are not responses.
- Motivation (wants, desires) are the states in which we want to obtain these gene-specified reinforcers – a unifying, Darwinian, theory.
- A reasoning, rational, syntactic system allows these gene-specified emotion-related reinforcers to be deferred in terms of longer-term goals in the interests of the individual, the phenotype.
- Correction of these first order syntactic thoughts requires a Higher Order Syntactic Thought system – and this HOST system is associated with consciousness.
- Decisions between the genotype and the phenotype (genes vs phenes), and the effects of noise in the brain on decision-making and on free will.

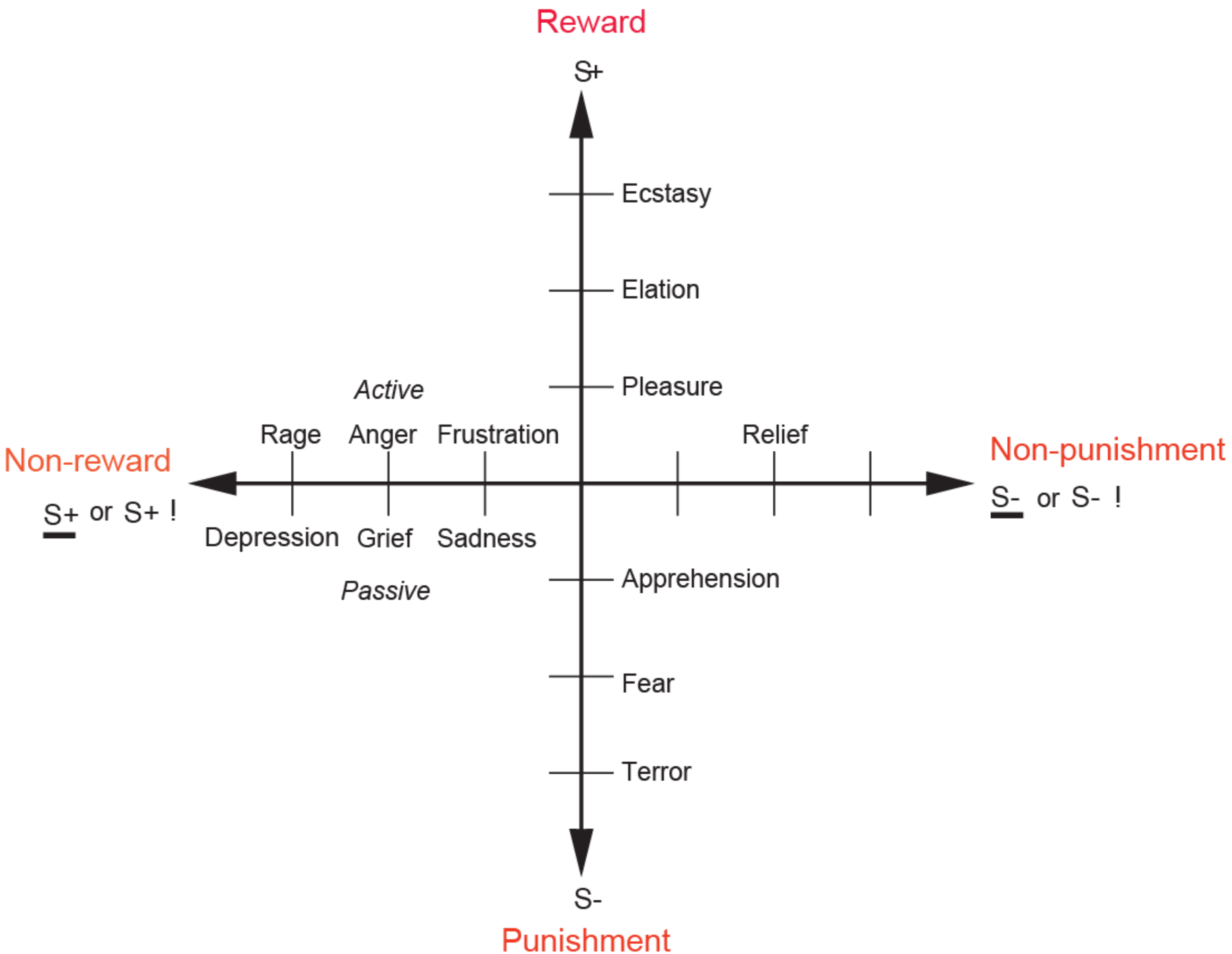
(E T Rolls. Emotion and Decision-Making Explained, 2014: Oxford)

Multiple routes for emotion-related responses

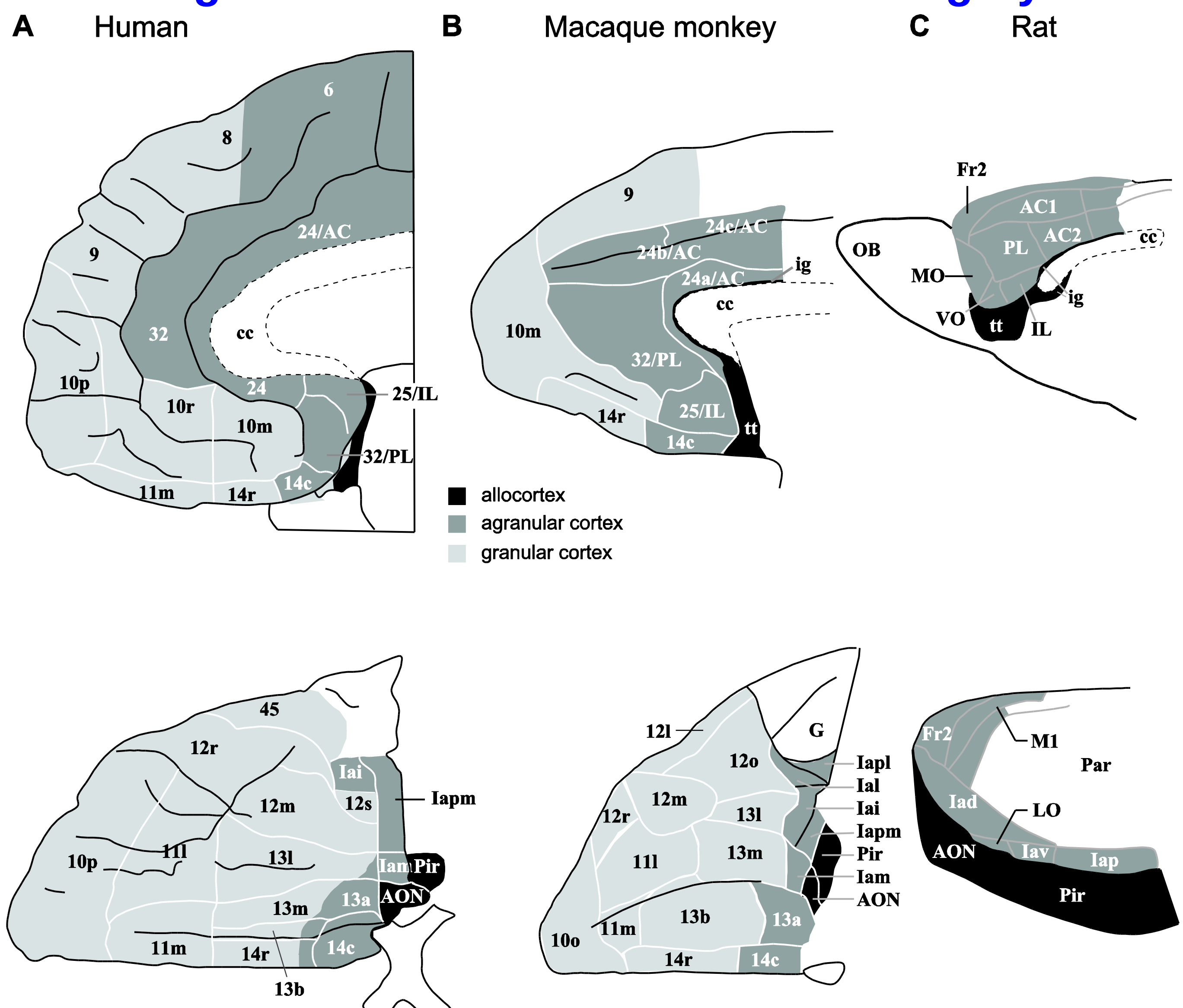


Rolls 2014 Emotion and Decision-Making Explained. Oxford

Emotions: States Elicited by Rewards and Punishers (instrumental reinforcing stimuli)

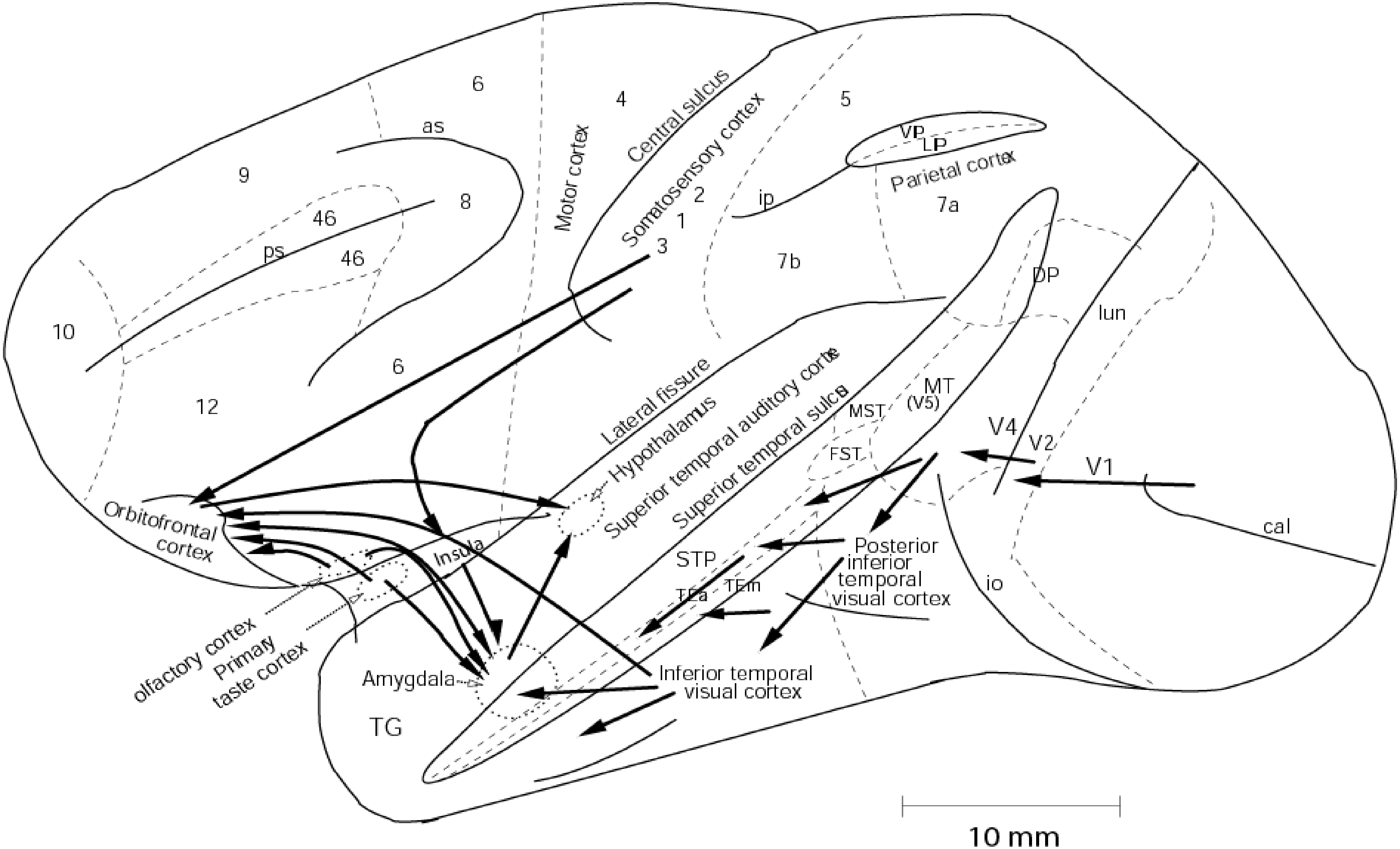


The orbitofrontal and cingulate cortices.
Agranular cortical areas are in dark grey.

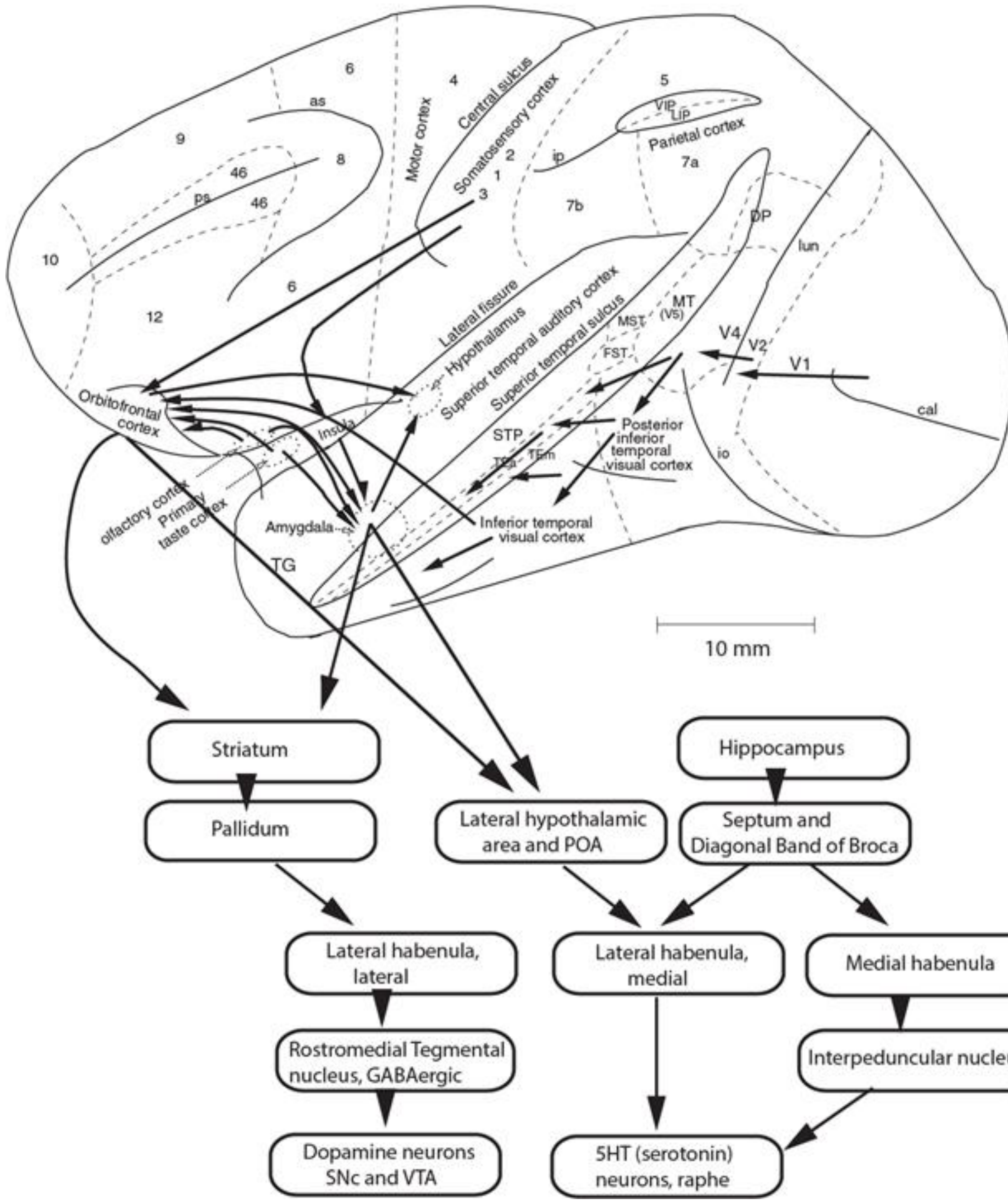


There may be no cortical area in rodents that is homologous to most of the primate including human orbitofrontal cortex: Wise (2008)

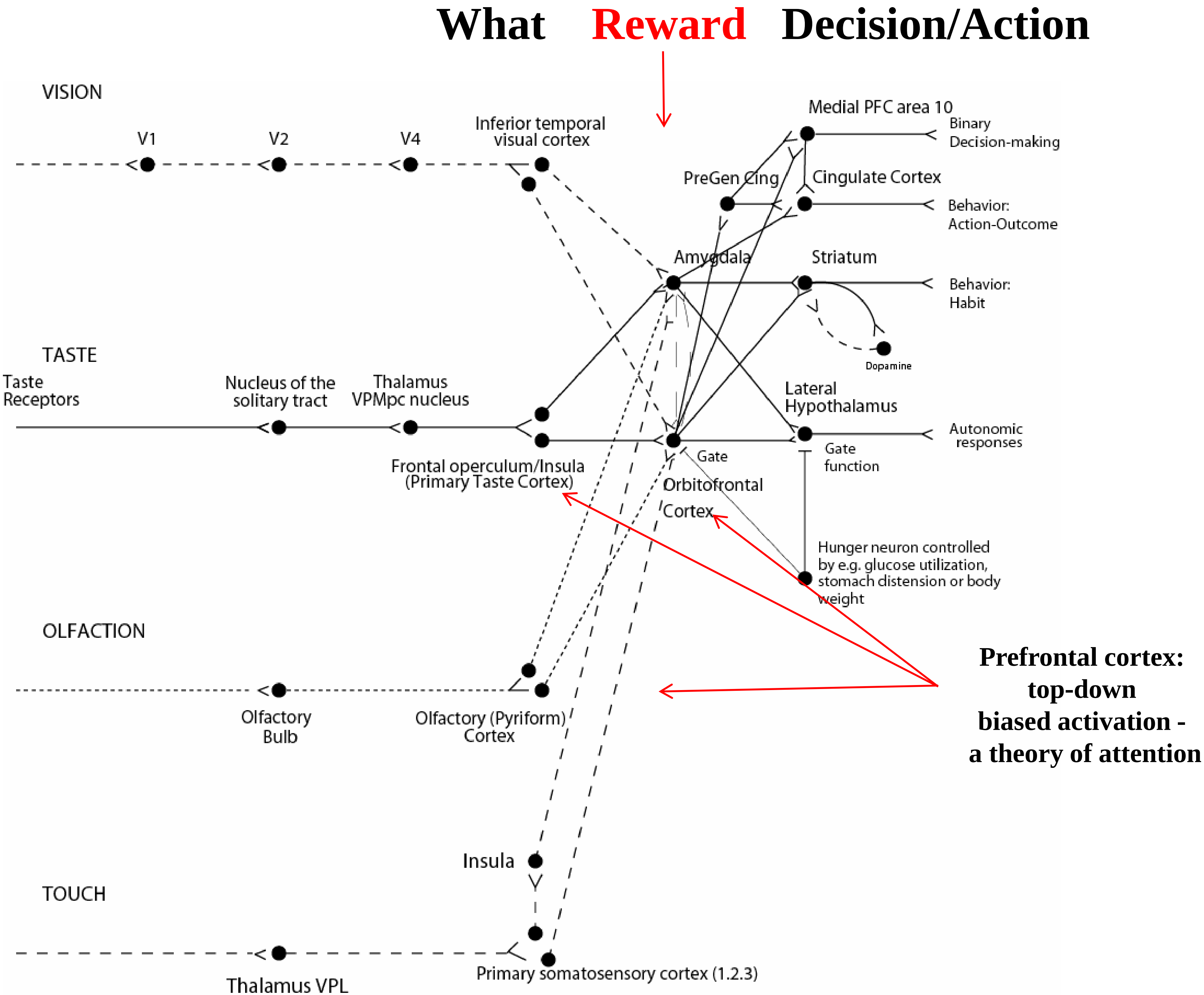
Taste, olfactory, somatosensory and visual inputs to the orbitofrontal cortex



Orbitofrontal cortex inputs, and some outputs

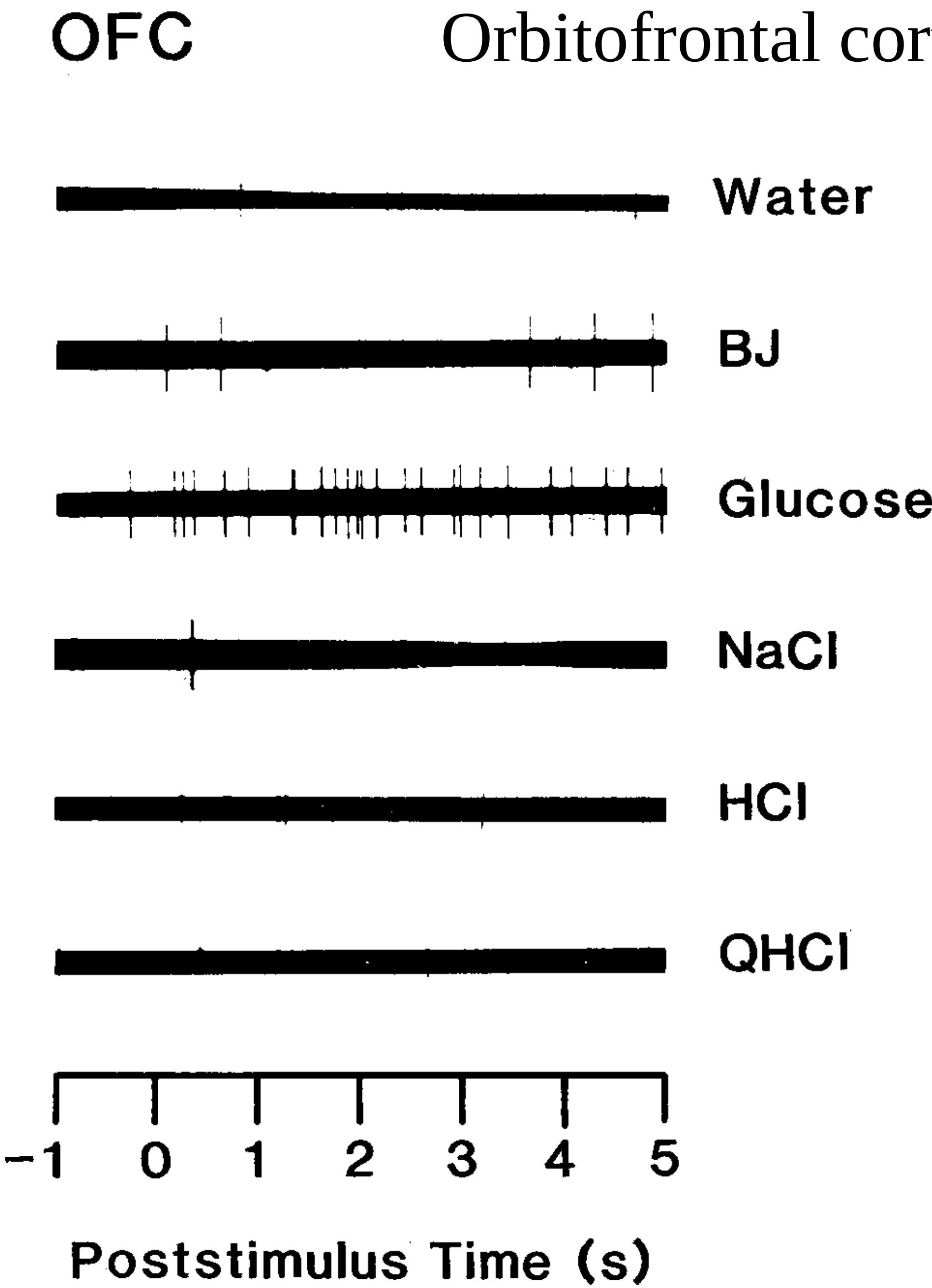


Rolls 2017 Neurosci Biobehav Rev

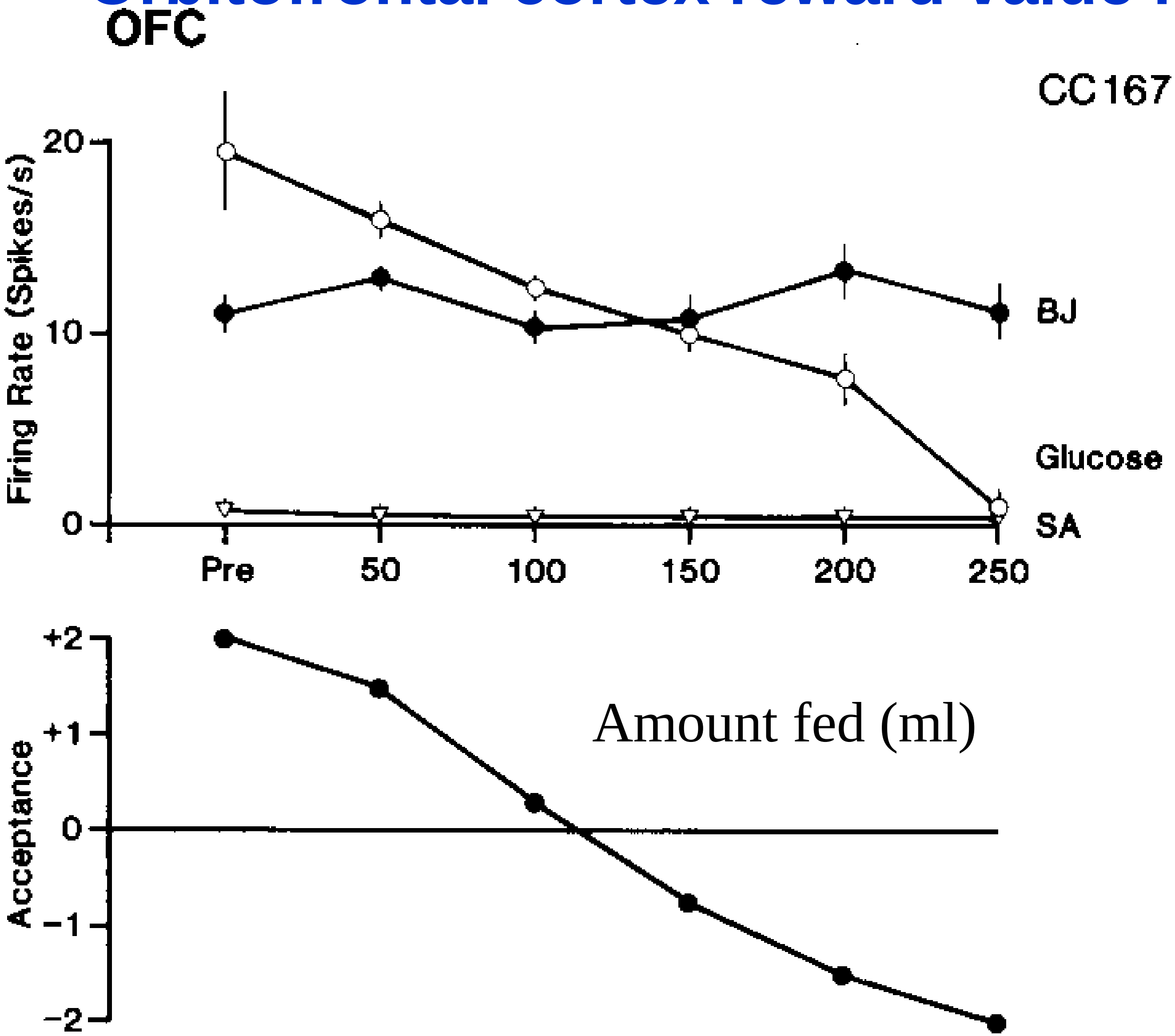


What
Reward
Decision/Action
VISION
V1
V2
V4
Inferior temporal visual cortex
Medial PFC area 10
Binary Decision-making
PreGen Cing
Cingulate Cortex
Behavior: Action-Outcome
Amygdala
Striatum
Behavior: Habit
Dopamine
TASTE
Taste Receptors
Nucleus of the solitary tract
Thalamus VPMpc nucleus
Lateral Hypothalamus
Autonomic responses
Gate
Gate function
Frontal operculum/Insula (Primary Taste Cortex)
Orbitofrontal Cortex
Hunger neuron controlled by e.g. glucose utilization, stomach distension or body weight
OLFACTION
Olfactory Bulb
Olfactory (Pyriform) Cortex
Prefrontal cortex: top-down biased activation - a theory of attention
Insula
TOUCH
Thalamus VPL
Primary somatosensory cortex (1.2.3)

Orbitofrontal cortex taste neuron



Orbitofrontal cortex reward value neurons

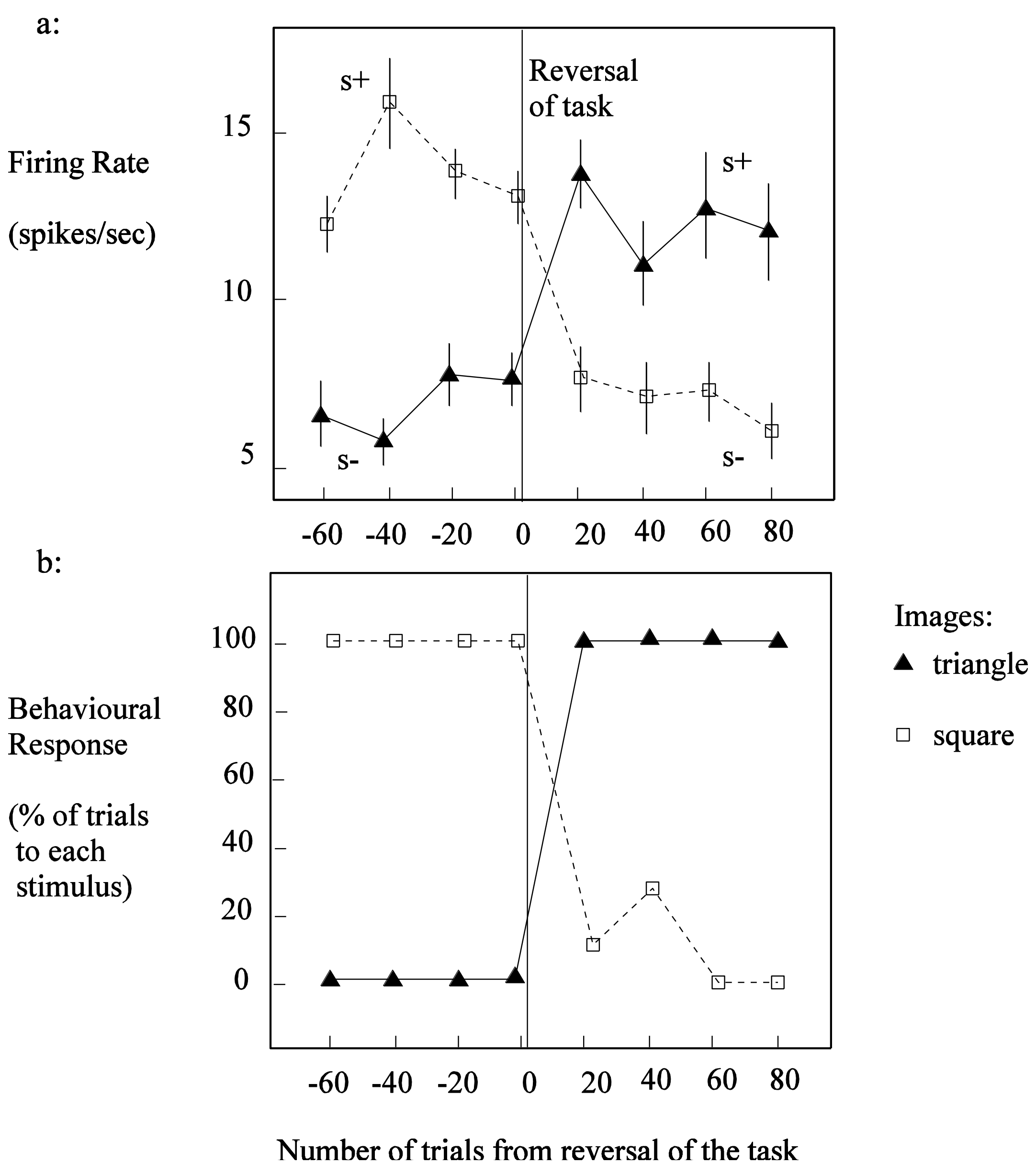


Sensory-specific satiety in the macaque orbitofrontal cortex

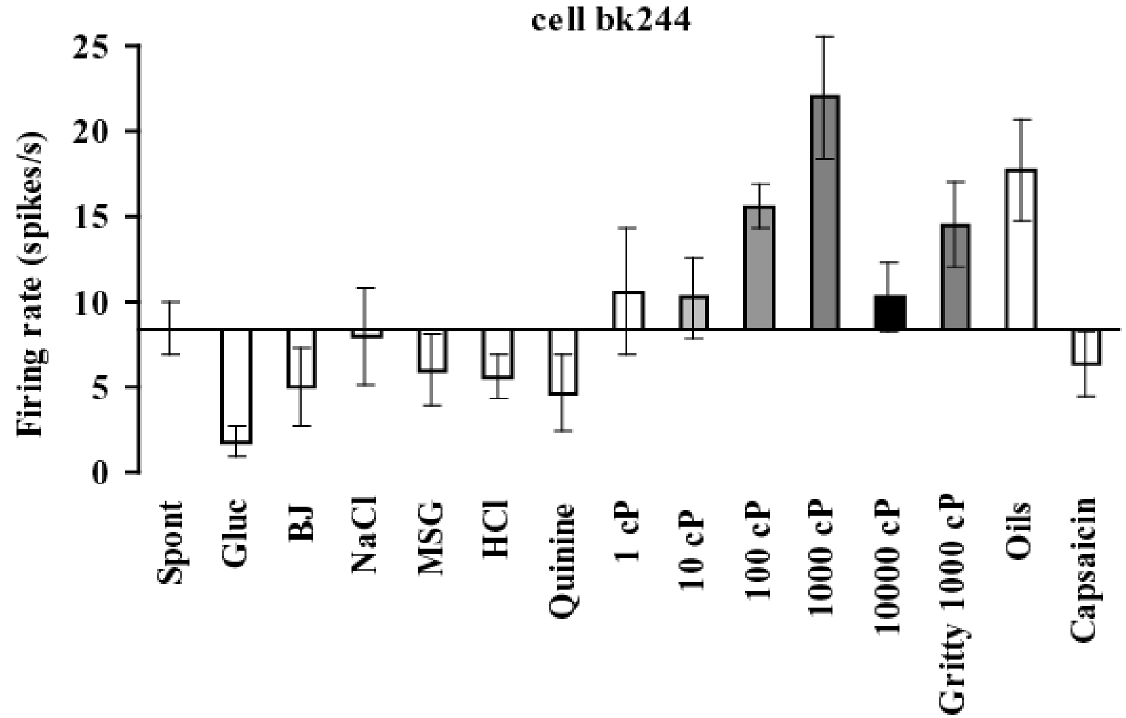
Rolls,E.T. et al (1989) European Journal of Neuroscience 1: 53-60.

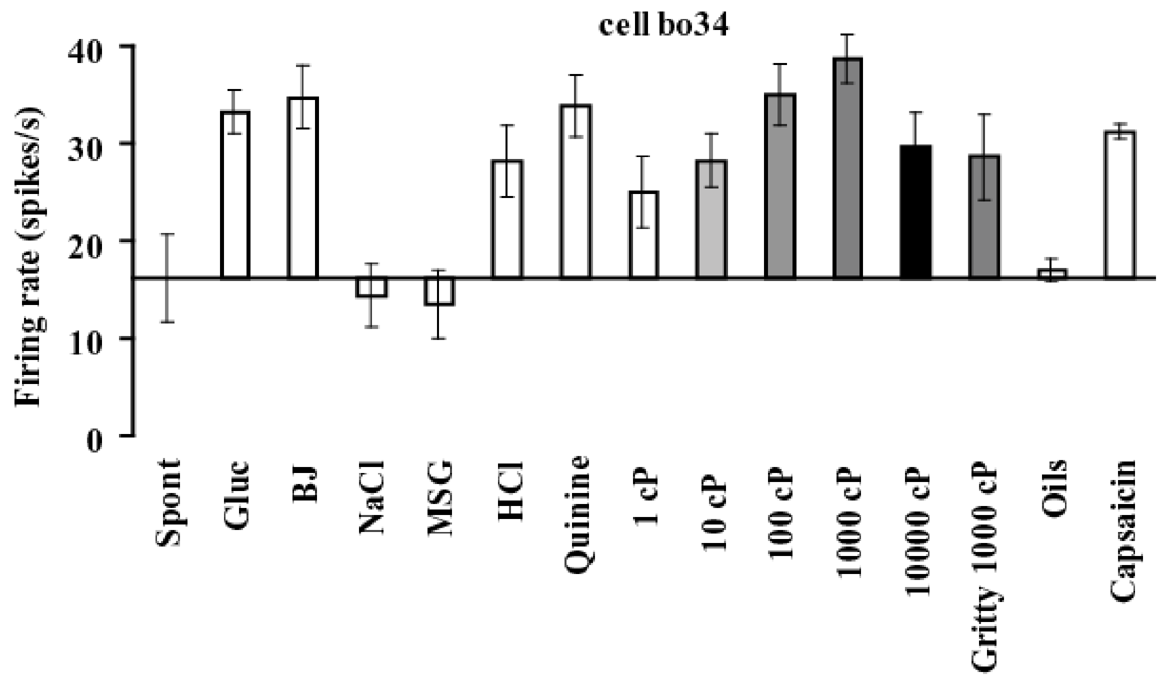
Orbitofrontal cortex neurons learn and reverse expected value

Visual to taste association learning and reversal



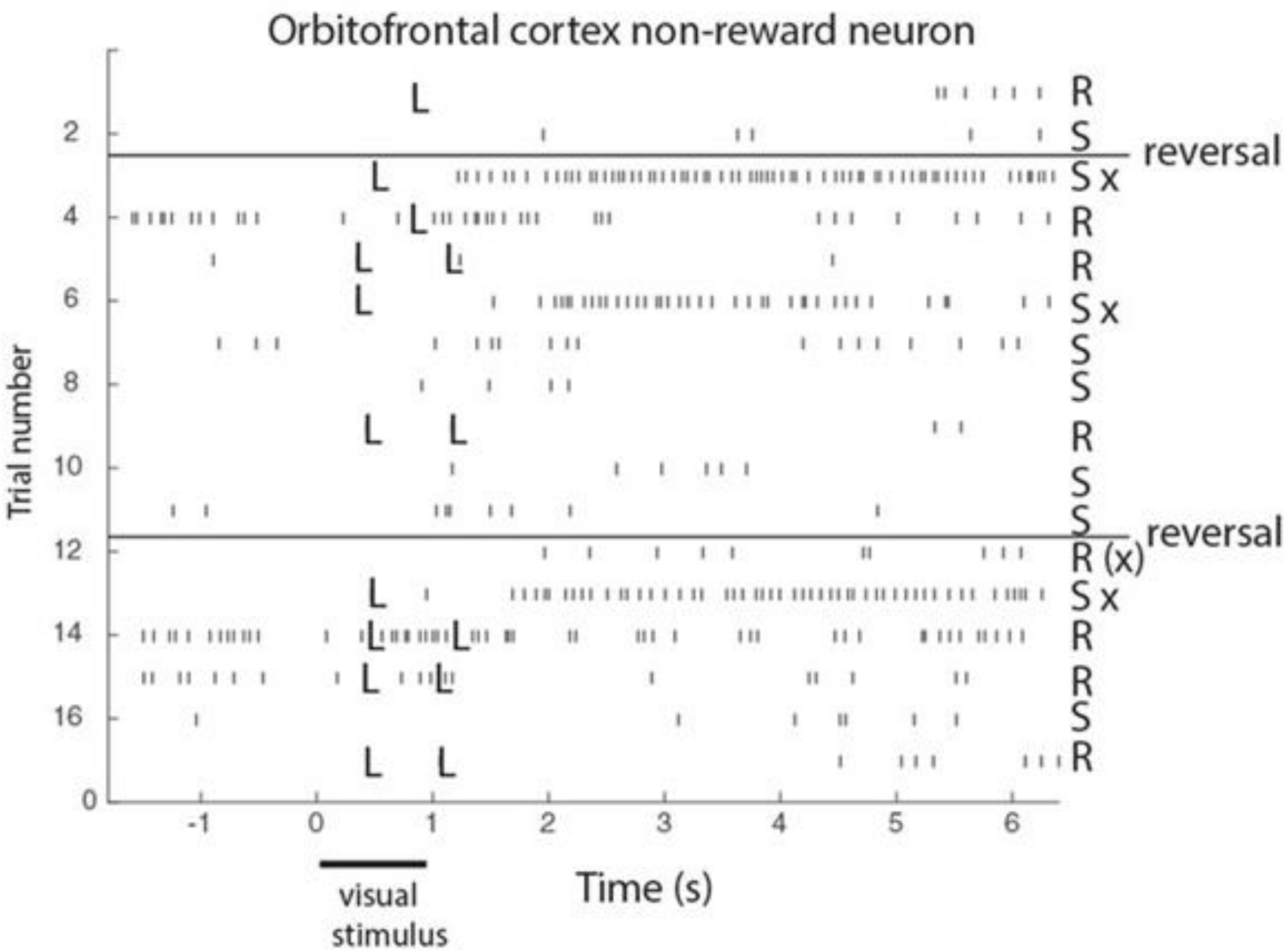
Orbitofrontal cortex representations of specific reward value:
Each orbitofrontal cortex neuron responds to a different combination of taste, odor, texture and temperature stimuli:
as a population they provide information about the specific reward value of many different stimuli.





Verhagen, Rolls and Kadohisa (2003) J Neurophysiology 90

Orbitofrontal cortex error neuron responding only in reversal in a visual-taste association task – when an expected reward was not obtained. Negative reward prediction error, maintained in an attractor



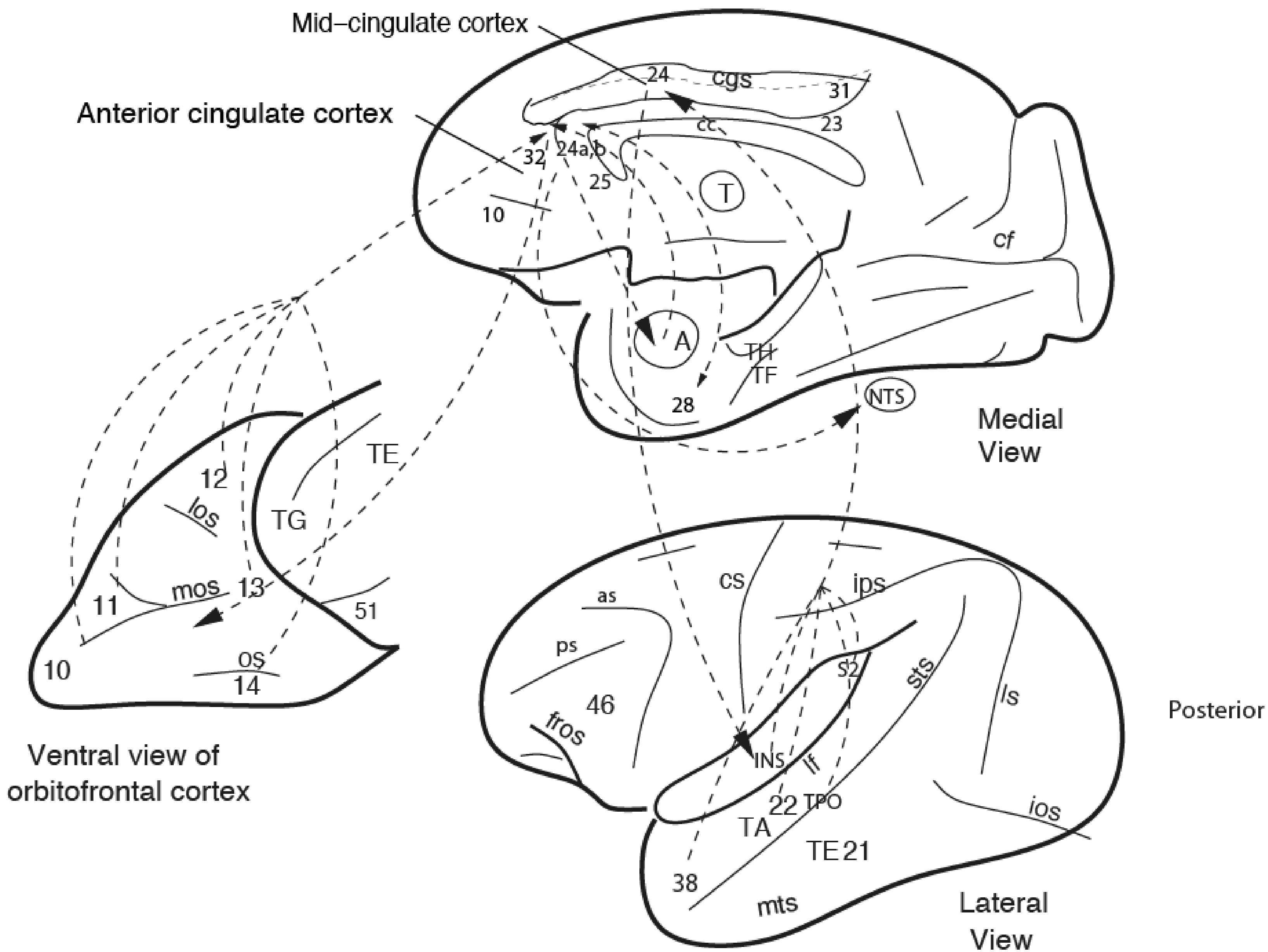
Thorpe, Rolls and Maddison 1983 Exp Brain Res

Orbitofrontal cortex neuronal responses

- **Taste reward. Only respond if hungry. Implement sensory-specific satiety.**
  - **All tastes are represented, including sweet, salt, bitter, sour and umami, and all are primary reinforcers.**
- **Olfactory reward.**
  - **Hunger dependent. Implement olfactory sensory-specific satiety.**
  - **40% reflect olfactory-taste association learning.**
- **Texture.**
  - **Reward - hunger dependent.**
  - **Fat texture. Fat is coded by texture, not by unsaturated fatty acids (eg linoleic)**
  - **Separate viscosity system. Separate astringency (tannic acid) system.**
- **Temperature.**
- **Visual**
  - **Reward. One-trial visual-to-taste association learning. Hunger dependent. Implement visual sensory-specific satiety.**
  - **Face-selective neurons**
- **Auditory, e.g vocalization**
- **Non-reward, error detection: “negative reward prediction error neurons”**
- **Activated from brain-stimulation reward sites**
- **High-dimensional representation of a very wide range of the sensory properties of both rewards and punishers, with secondary reinforcers linked to primary by stimulus-reinforcement association learning and reversal.**
- **A neuronal representation of stimulus value not of actions (cingulate) or habit responses (striatum). Used for one-trial reward value reversal.**

Rolls 2015 Progress in Neurobiology; Rolls 2017 Neuropsychologia

Anterior cingulate cortex: action-outcome learning

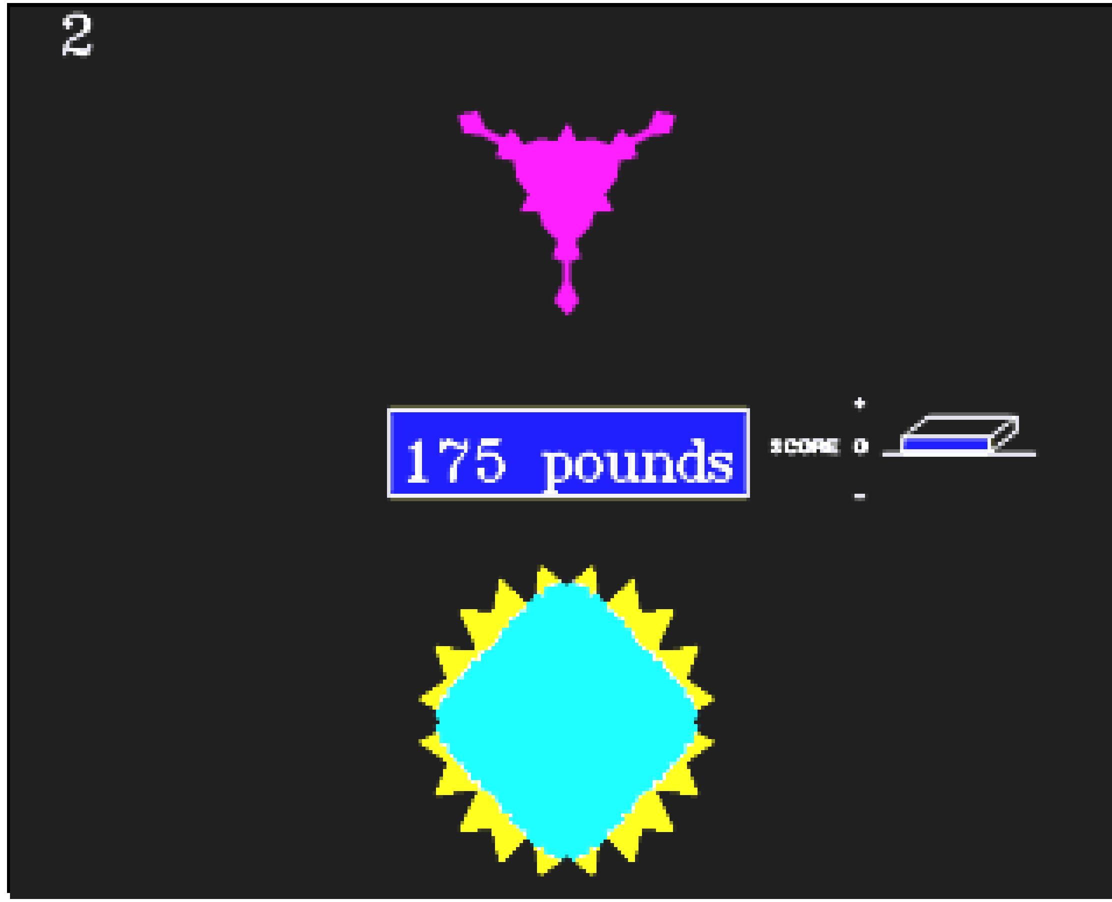


Reward value representations in humans and neuroeconomics: fMRI

- Is the human OFC involved in representing abstract punishment such as losing money?
- If so, are the representations for monetary reward and punishment separate and distinct in the OFC or overlapping?
- How is the magnitude of the monetary reward and loss represented?

Task Description

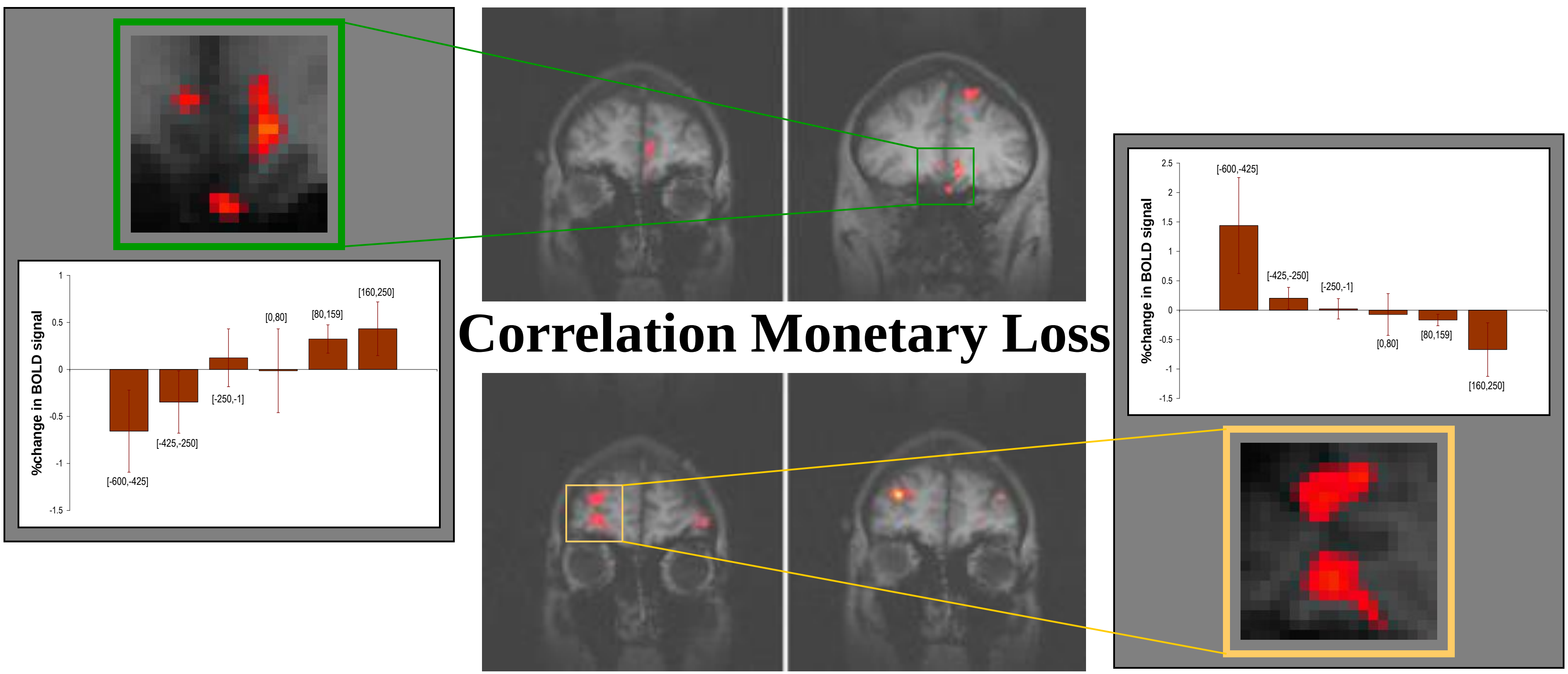
- Two Unfamiliar Fractals
- Random Position
- S+/S– = probabilistic gain/loss
- Choose S+ to
  maximise gain
- Reversal



Neuroeconomics

Reciprocal relation between the medial OFC for reward and the lateral OFC for non-reward / loss / punishment

Correlation Monetary Reward



O'Doherty, Kringelbach, Rolls, Hornak and Andrews (2001)
Abstract reward and punishment representations in the human orbitofrontal cortex.
Nature Neuroscience 4: 95-102.

Conclusions: Economic Value in the human orbitofrontal cortex

- Activations in the medial orbitofrontal cortex are proportional to the monetary reward value gain.

- Activations in the lateral orbitofrontal cortex are proportional to the monetary value loss.

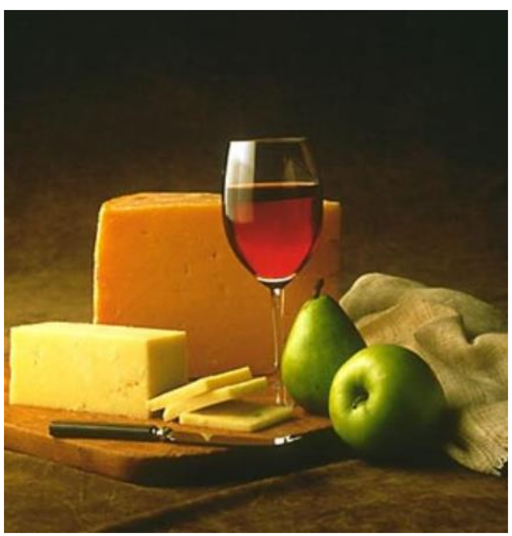
- Economic Value is represented in the human orbitofrontal cortex.

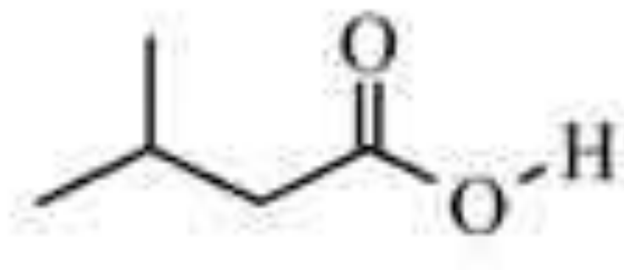
O'Doherty, Kringelbach, Rolls, Hornak and Andrews (2001)
Abstract reward and punishment representations in the human orbitofrontal cortex.
Nature Neuroscience 4: 95-102.

Conclusions: A visually presented word label modulates representations of odors in reward value areas in the orbitofrontal cortex, amygdala, and ventral striatum. Cognition can influence subjective, conscious, affective representations in the orbitofrontal and pregenual cingulate cortices.

Isovaleric Acid

Cheddar Cheese



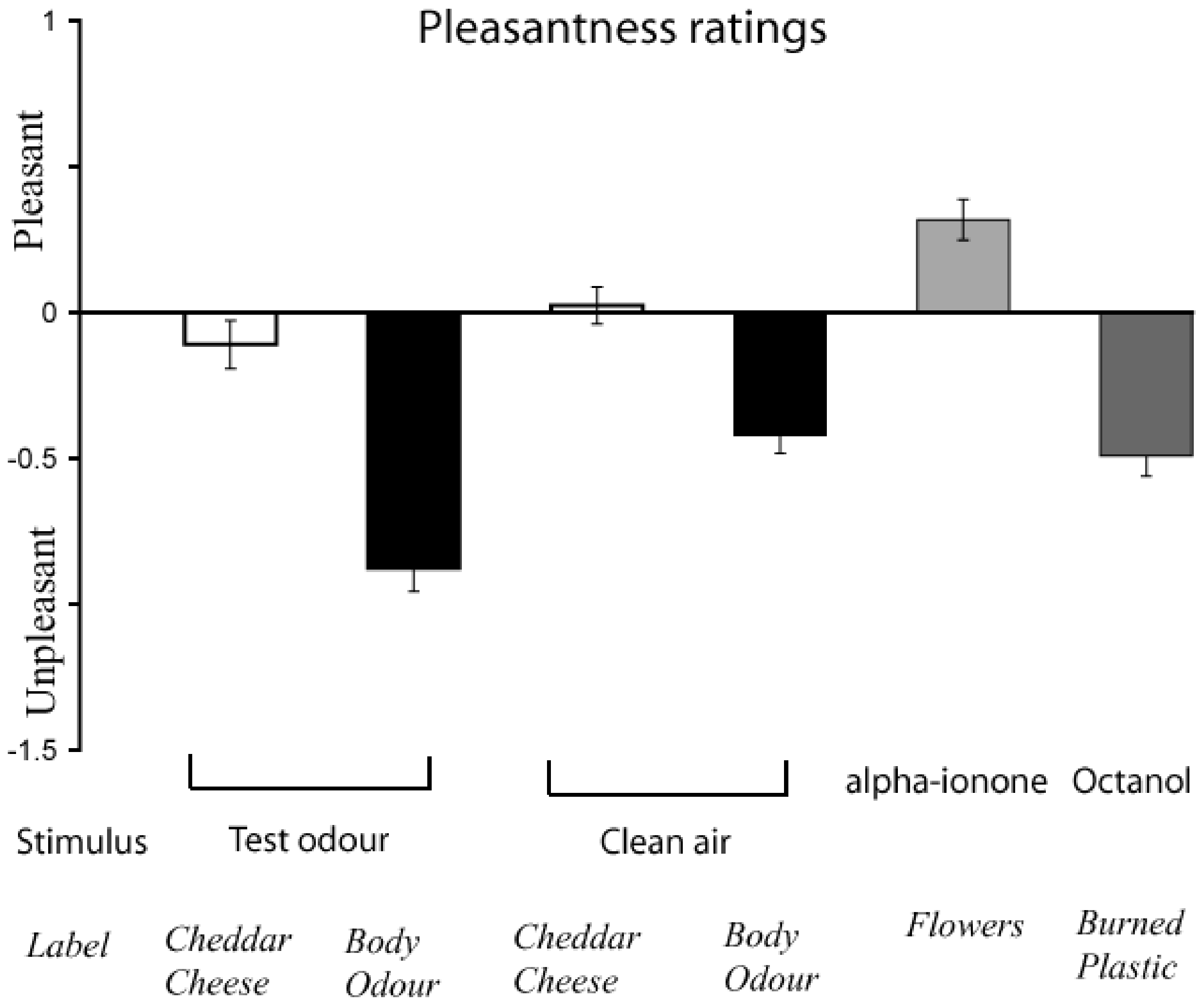


$(CH_3)_2CHCH_2COOH$

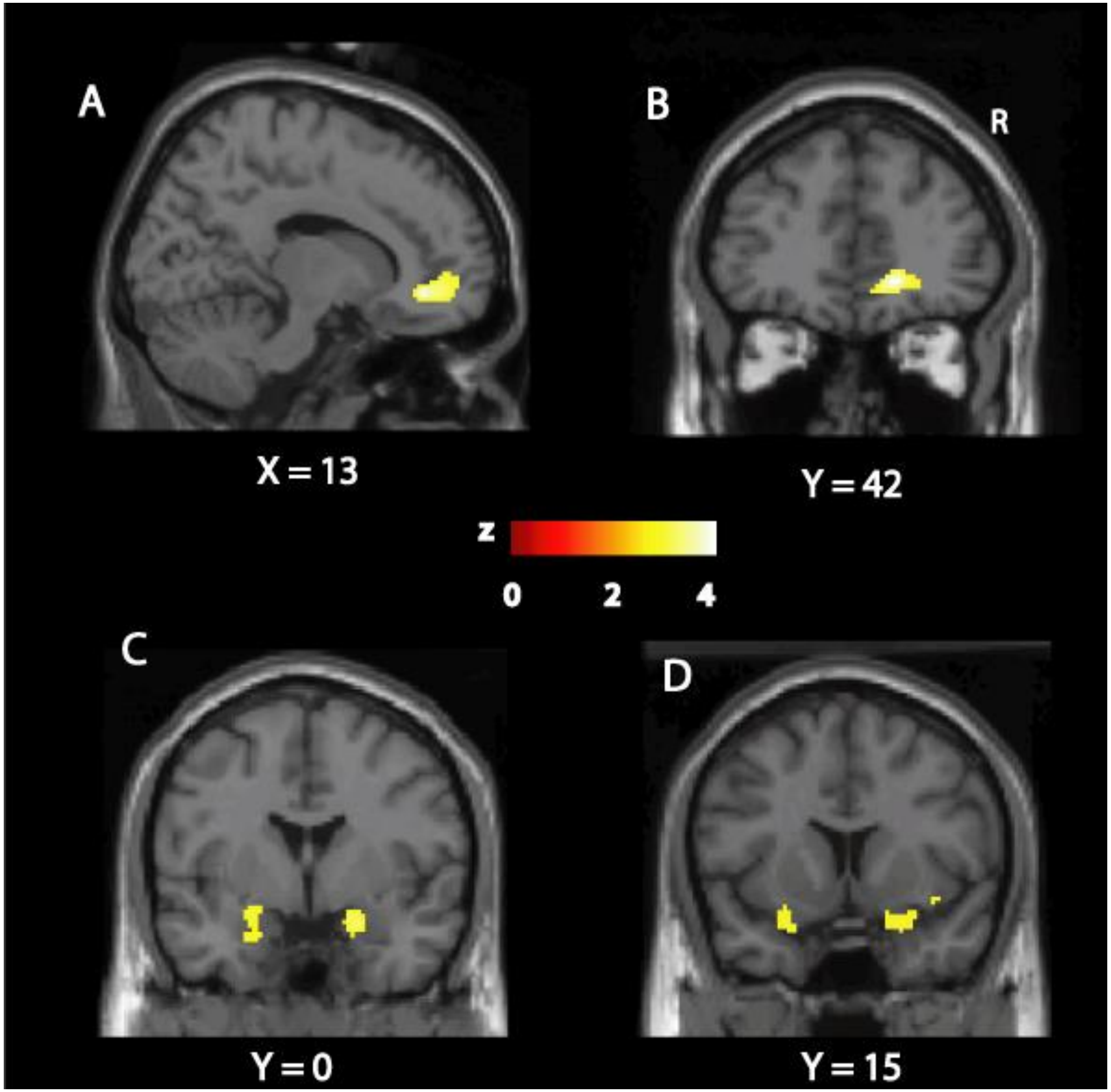
Body odour

De Araujo,I.E.T., Rolls,E.T., Velazco,M.I., Margot,C. and Cayeux,I. (2005) Cognitive modulation of olfactory processing. Neuron 46: 671-679.

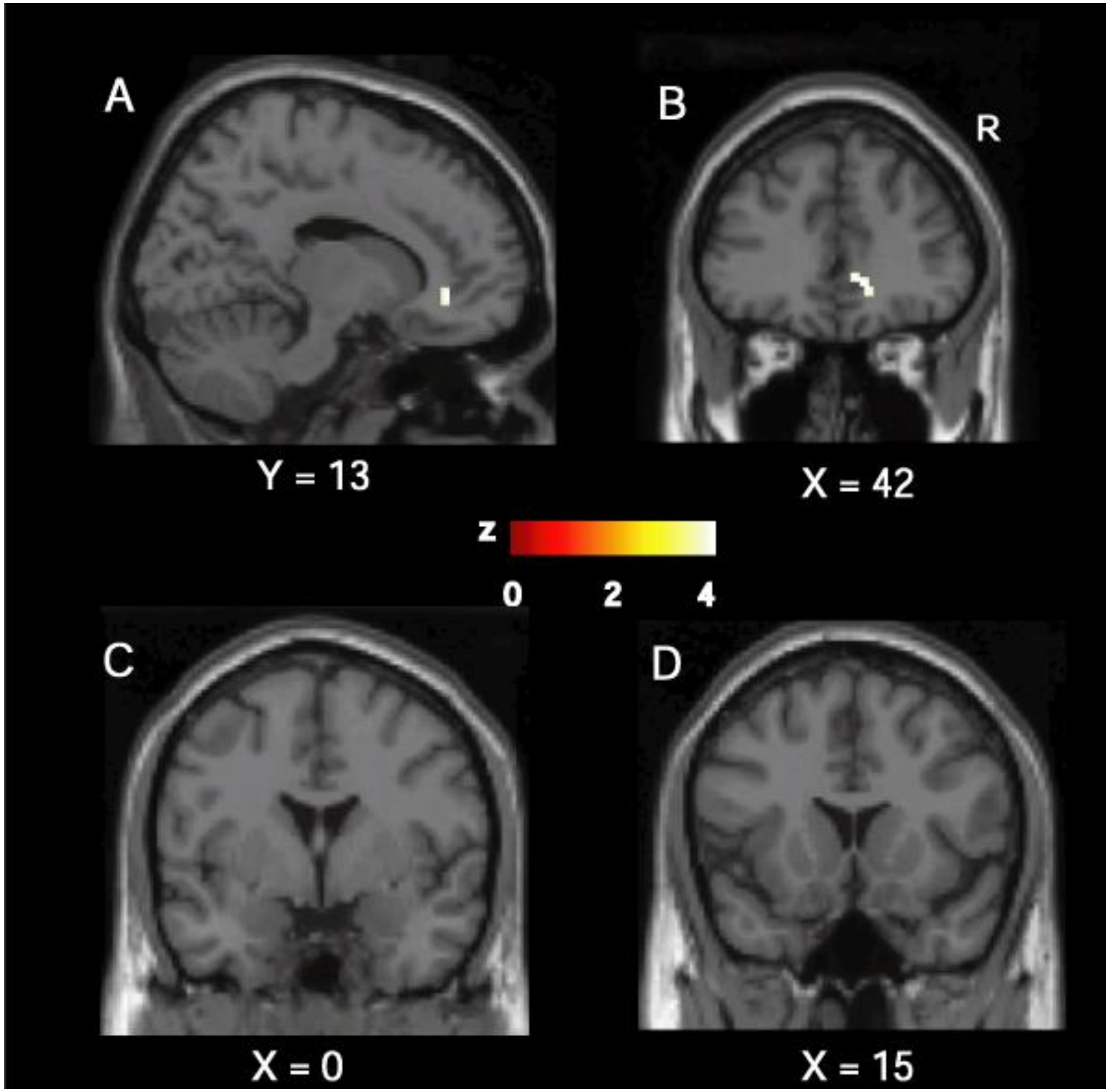
Effect of visually presented words (‘cheddar cheese’ vs ‘body odor’) on responses to a single Test odor, isovaleric acid



Cognitive modulation revealed by a correlation between the BOLD signal and the pleasantness ratings given to the Test odour.
A, B: anterior cingulate; C: amygdala; D: olfactory tubercle



Correlation analysis of BOLD signal with pleasantness ratings given to Clean Air. A, B: anterior cingulate; C: amygdala; D: olfactory tubercle

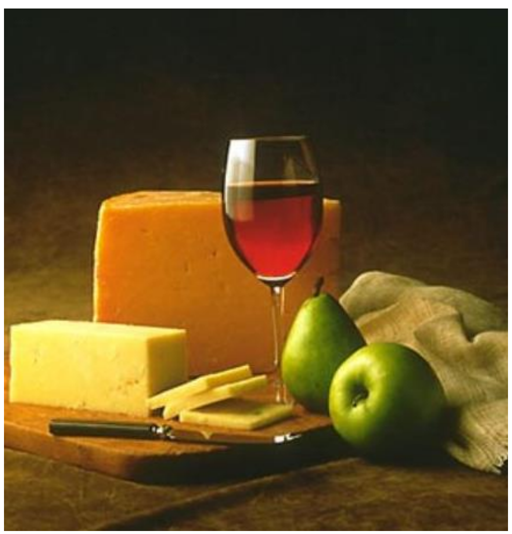


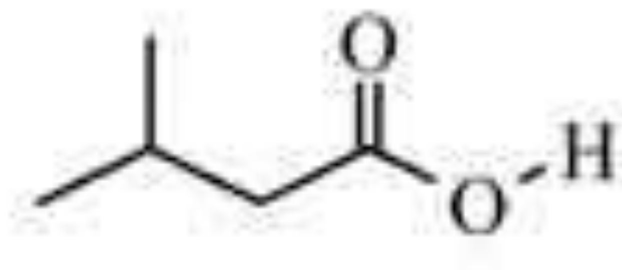
Conclusions: A visually presented word label modulates representations of odors in olfactory areas in the orbitofrontal cortex, amygdala, and olfactory tubercle. Cognition can influence subjective, conscious, affective representations in the orbitofrontal and pregenual cingulate cortices.

Isovaleric Acid

Cheddar Cheese

Body odour





$(CH_3)_2CHCH_2COOH$

De Araujo,I.E.T., Rolls,E.T., Velazco,M.I., Margot,C. and Cayeux,I. (2005) Cognitive modulation of olfactory processing. Neuron 46: 671-679.

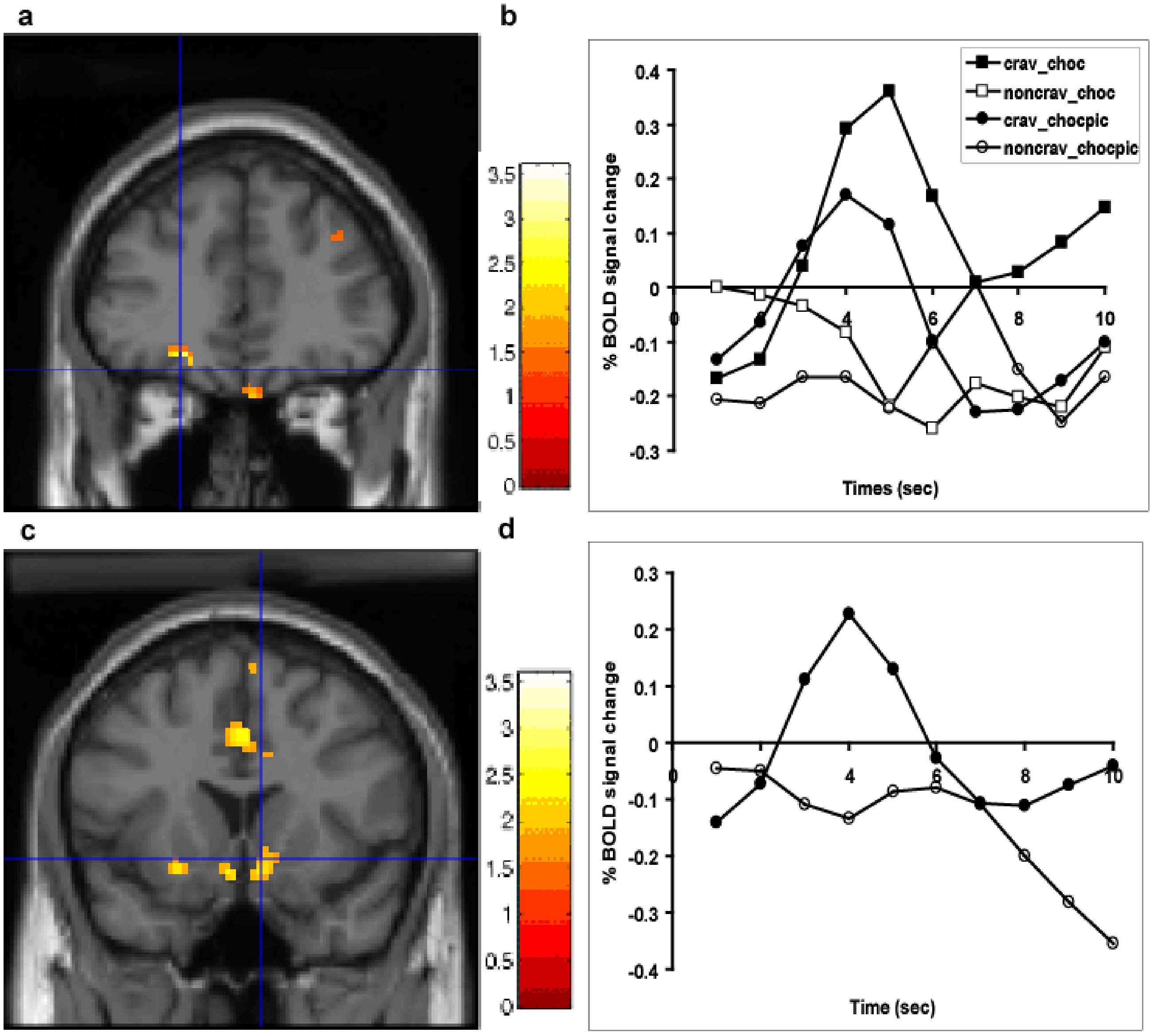
Do responses of the orbitofrontal cortex and pregenual cingulate cortex enable individual differences in affective behaviour and decision-making to be predicted? Chocolate craving: a craving and a non-craving group

- **Chocolate in the mouth – flavour differences?**
- **Sight of chocolate – conditioned cue differences?**
- **Sight of chocolate and chocolate in the mouth – greater supralinearity?**
- **Cognitive biasing: dark chocolate word label vs white chocolate word label**
- **Condensed milk – similar texture and sweetness to chocolate, but not craved.**
- **Tasteless control solution**
- **8 cravers and 8 non-craver participants.**
- **SPM fMRI group random effects analysis with full correction or svc.**

Rolls and McCabe (2007) European Journal of Neuroscience 26

Sight of chocolate

Sight of dark chocolate only: cravers vs non-cravers



a. More activation of mid and medial orbitofrontal cortex in cravers than non-cravers

c. More activation in the ventral striatum in cravers than non-cravers

fMRI of chocolate craving:
individual differences in brain activations predict craving and food intake

- There were no differences between chocolate cravers and non-cravers in responses to the flavour of chocolate in the primary taste cortex. Moreover the activations in the primary taste cortex were not correlated with the pleasantness or wanting ratings for chocolate. Thus it was not differences in the primary taste cortex, or physical sensitivity to taste and oral texture, that separated the cravers from the non-cravers.
- The flavour of chocolate produced more activation in cravers than non-cravers in the medial orbitofrontal cortex.
- The sight of chocolate produced more activation in chocolate cravers in the medial orbitofrontal cortex (OFC) and ventral striatum.
- A combination of the sight and flavour of chocolate produced more activation than the sum of the components in the medial orbitofrontal cortex, pregenual cingulate cortex, and striatum.
- This non-linearity was greater in the cravers than the non-cravers.
- The subjective pleasantness ratings of the chocolate and chocolate-related stimuli had higher positive correlations with the fMRI BOLD signals in the pregenual cingulate cortex and medial OFC in the cravers than in the non-cravers.
- The amount of chocolate eaten on a regular basis was higher in the cravers (370 g / week) than the non-cravers (22 g / week).
- Understanding individual differences in brain responses to very pleasant foods helps to understand the mechanisms that drive the liking for foods, and thus food intake and decision-making. Individual differences and personality.

Rolls and McCabe (2007) European Journal of Neuroscience 26: 1067-1076

Personality and reward systems in the brain

- Each specific type of reward (taste, flavour, water, touch …) is represented by different neurons.
- Each specific type of gene-specified reward is subject to variation between individuals as part of evolution by natural selection.
- Therefore different individuals may have different sensitivity to different specific types of reward, non-reward, etc.
- This variation may contribute to personality, and to high dimensionality of the space.
- This may be reflected in differential sensitivity in different individuals in how brain reward systems respond to different reinforcers.

Orbitofrontal cortex neuroimaging

- **Taste : Both pleasant and unpleasant tastes are represented**
  - **Amygdala: pleasant tastes are as much represented as unpleasant tastes**
- **Olfactory reward. Olfactory sensory-specific satiety.**
- **Olfaction: pleasant odours activate a particular region of the OFC**
  - **Anterior cingulate cortex is activated by pleasant and by unpleasant odors**
  - **Primary olfactory cortical areas represent the identity and intensity of odours**
  - **Cognitive inputs, word labels, modulate olfactory effects in the OFC and ant cingulate.**
- **Whole food: taste, odor and texture**
  - **Reward – reflects sensory-specific satiety.**
  - **Correlation of OFC activation with the subjective pleasantness of the food**
- **Oral viscosity and fat texture: insula and orbitofrontal cortex**
- **Flavour: olfactory-taste convergence**
  - **In the orbitofrontal cortex and adjoining agranular insula; MSG+savoury odor**
  - **The primary taste cortex in the insula is unimodal**
- **Individual differences: chocolate craving: orbitofrontal cortex and pregenual cingulate**
- **Somatosensory pleasure and pain more than neutral**
  - **Correlation of OFC activation with subjective pleasantness and pain**
  - **Anterior cingulate cortex: anterior - pleasant touch; mid - pain**
- **Abstract (monetary) reward and punishment (loss) in a reversal task**
  - **Separate representations of the magnitude of the gain (medial) and loss (lateral)**
  - **Expected value in a probabilistic task: Activation = probability x reward value**
- **Face reversal cued by changing face expression: reward prediction error**
  - **OFC activation related to an angry expression when it is used as a reversal cue**
  - **Activation in the fusiform face area does not reflect the reversal**
- **Amphetamine activates the medial orbitofrontal cortex**
- **Cognitive affective modulation of taste, flavour, odour and touch is implemented in the orbitofrontal and pregenual cingulate cortex.**

Reward and Non-Reward processing in the brain, and Depression

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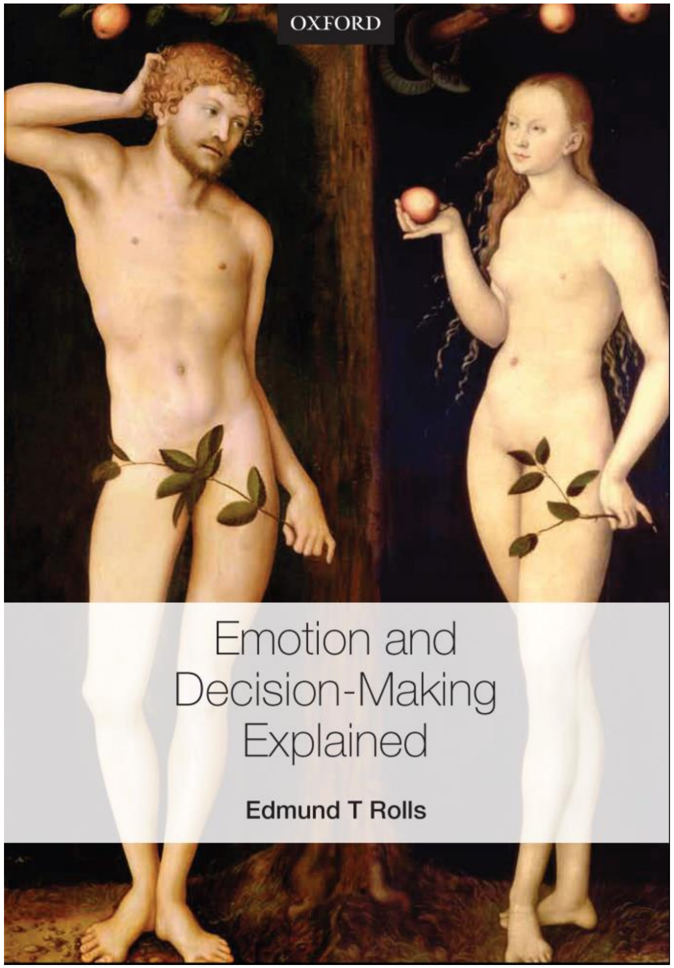
Uffizi, Florence

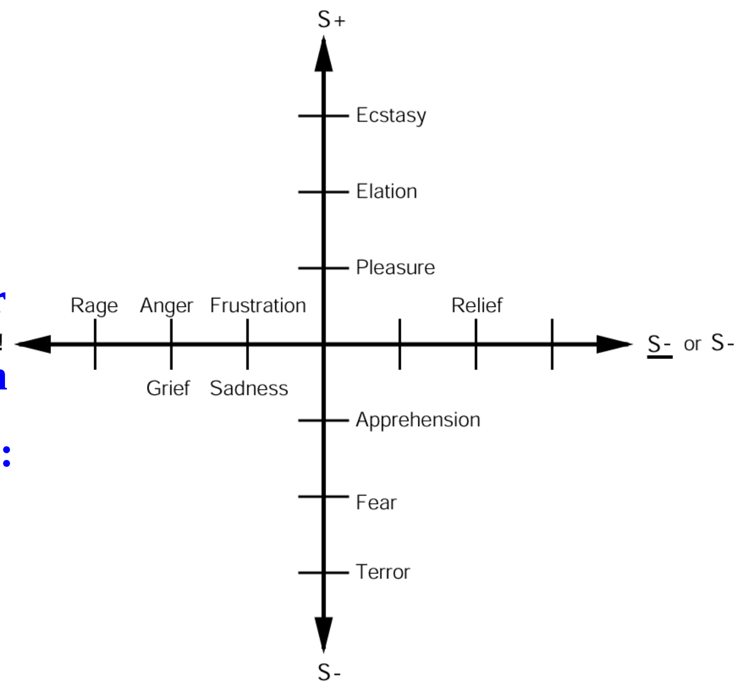


Oxford University Press 2014

Emotions: States Elicited by Rewards and Punishers

Reward

Omission or Termination of a Reward: can produce depression

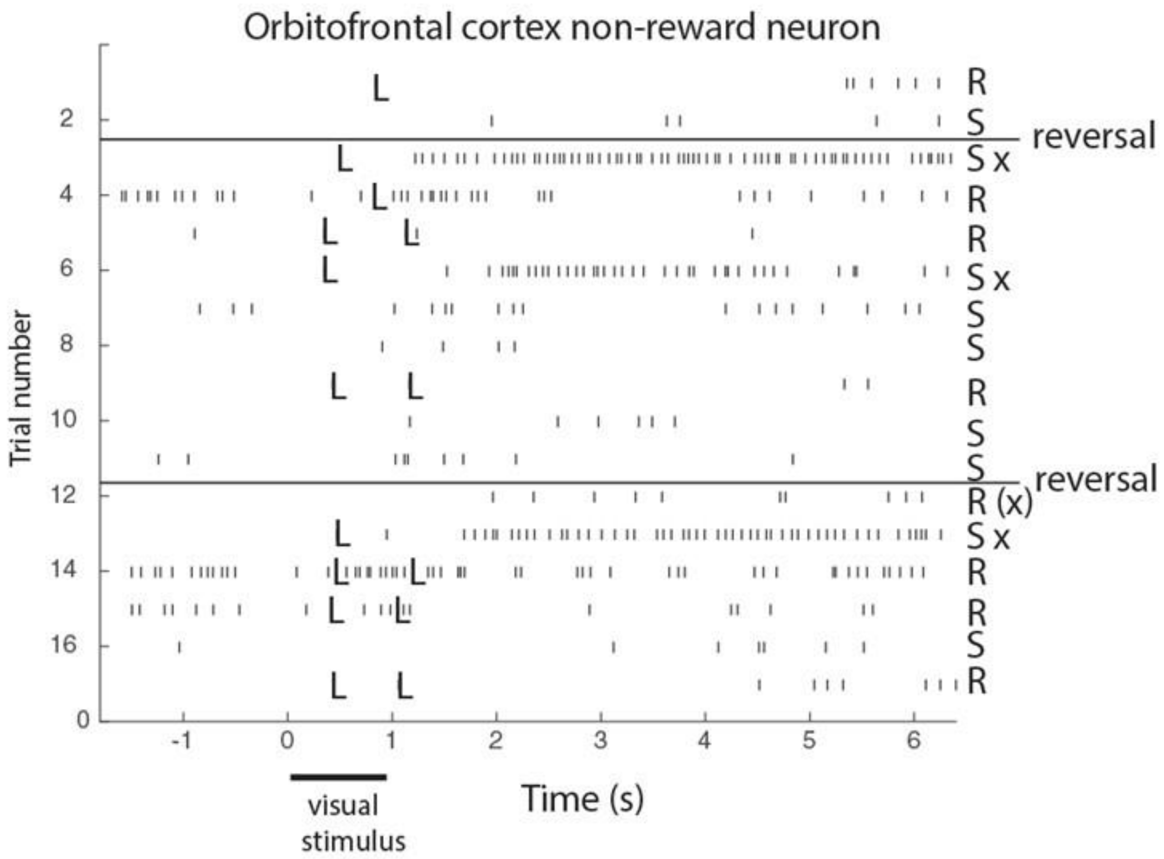


Omission or Termination of a Punisher

Punisher

A non-reward attractor theory of depression

- **The orbitofrontal cortex contains error neurons that respond to non-reward for many seconds in an attractor state that maintains a memory of the non-reward.**
- **Measured on reversal trials in visual discrimination reversal in macaques by Thorpe, Rolls and Maddison (1983).**



Rolls 2016 Neuroscience and Biobehavioral Reviews

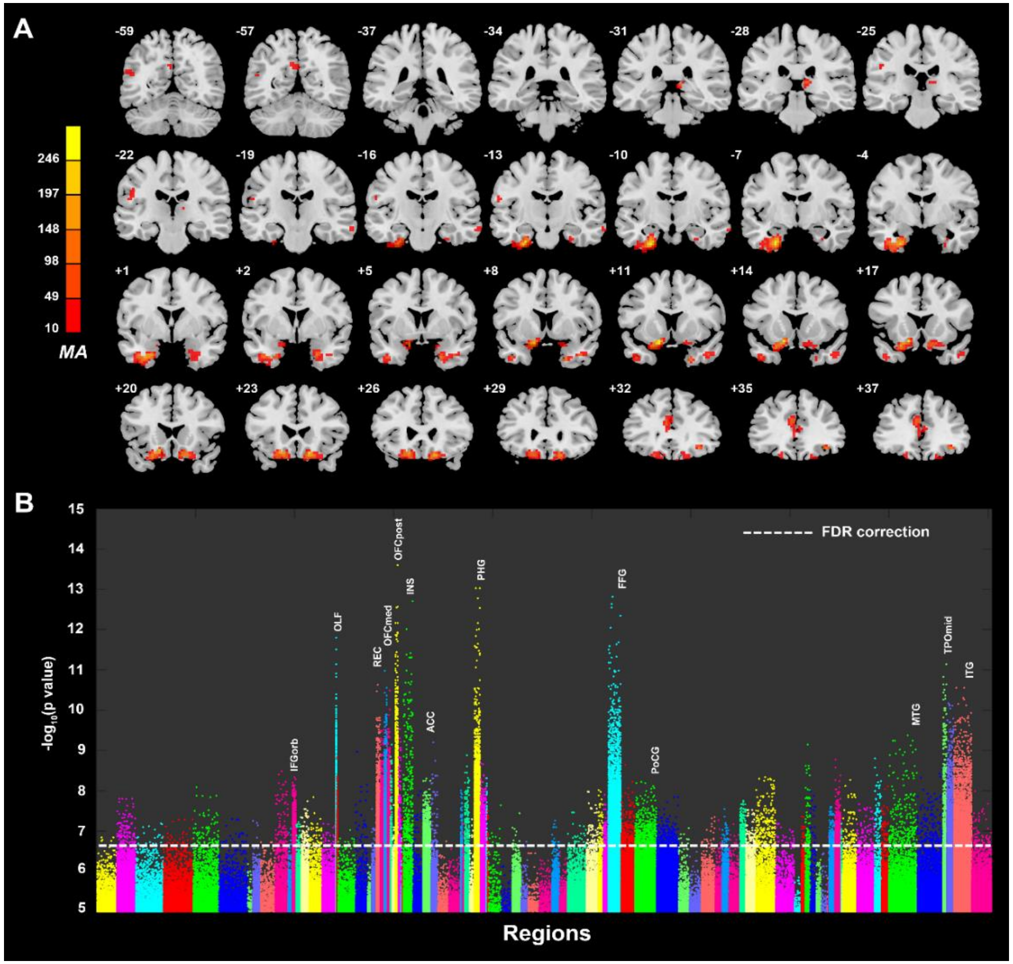
Functional connectivity in depression

- The first Brain-Wide voxel-level resting state functional-connectivity neuroimaging analysis of depression – BWAS (Brain-Wide Association Study).
- Big data, and multicenter collaboration, with 421 patients with major depressive disorder and 488 controls, were used to obtain statistically significant measures of voxel-level functional connectivity.
- Resting state functional connectivity between different voxels reflects correlations of activity between those voxels, and is a fundamental tool in helping to understand the brain regions with altered connectivity and function in depression.
- Each resting-state fMRI image included 47,619 voxels. For each pair of voxels, the time series were extracted and their correlation was calculated for each subject. Two-tailed, two-sample t-tests were performed on the 1,133,760,771 (47619×47618/2) functional connectivities between every pair of voxels.
- For the functional connectivity of a pair of voxels to be treated as significantly different ($p<0.01$) after FDR correction between patients and controls, the significance level uncorrected had to be $\mathrm{p} < 2.52 \times 10^{-7}$.

Cheng, Rolls et al 2016 Brain

Functional connectivity in depression

- Voxels in the medial and lateral orbitofrontal cortex, parahippocampal cortex, and precuneus with significantly different functional connectivity in depression.

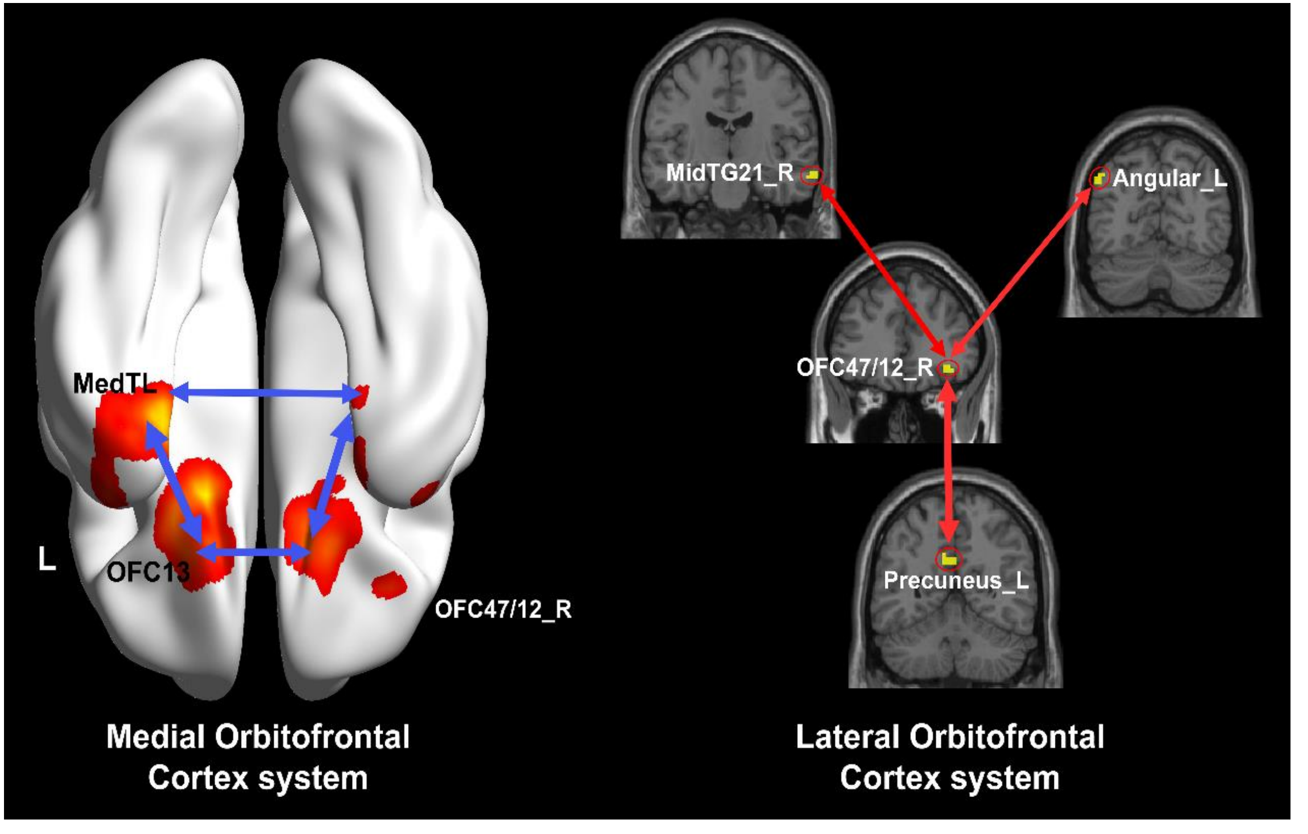


- P values of voxels in different brain regions. The horizontal line shows the significance level after FDR correction.

Cheng, Rolls et al 2016 Brain

Functional connectivity in depression

- Summary: In depression:
- Increased functional connectivity (red) between the lateral orbitofrontal cortex (related to non-reward) and the precuneus (related to the sense of self), the temporal cortex (vision), and the angular gyrus (language).
- Decreased functional connectivity between the medial orbitofrontal cortex (related to reward) and the parahippocampal gyrus memory-related areas.



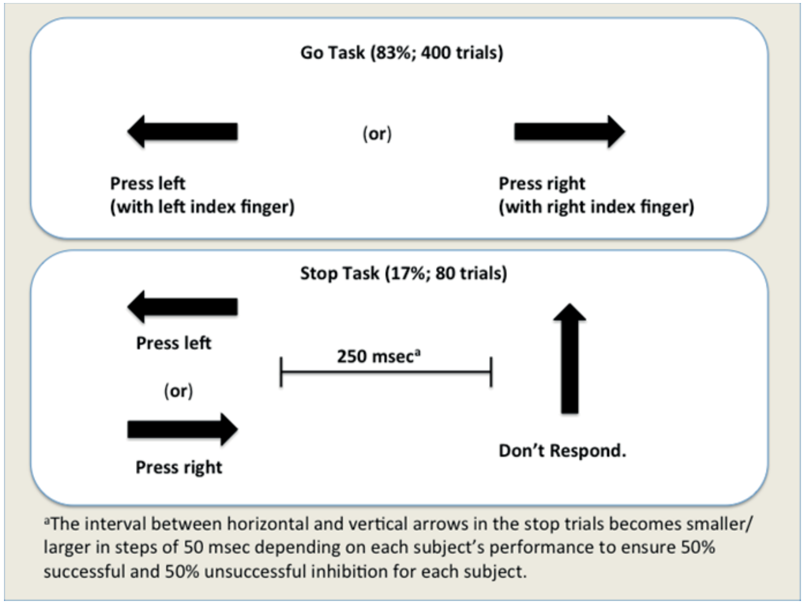
Cheng, Rolls et al 2016 Brain

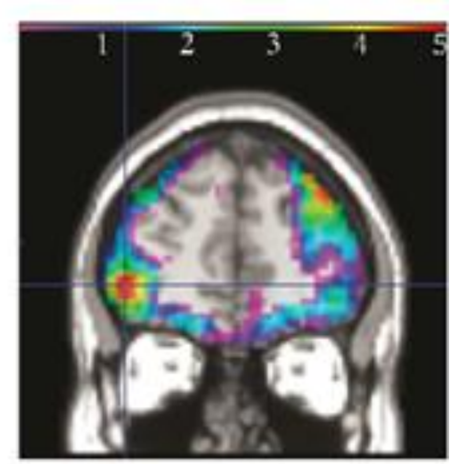
Depression

- **The reduced functional connectivity of the medial orbitofrontal cortex, implicated in reward, with memory systems provides a new way of understanding how memory systems may be biased away from pleasant events in depression.**
- **The increased functional connectivity of the lateral orbitofrontal cortex, implicated in non-reward and punishment, with areas of the brain implicated in representing the self, language, and inputs from face and related perceptual systems provides a new way of understanding how unpleasant events and thoughts, and lowered self-esteem, may be exacerbated in depression.**
- **Relating the changes in cortical connectivity to our understanding of the functions of different parts of the orbitofrontal cortex in emotion helps to provide new insight into the brain changes related to depression.**
- **The ‘big data’ brain-wide association study (BWAS) approach allowed voxel-level analysis, with significant links FDR corrected found between 47,619 voxels with 1,133,760,771 correlations between pairs of voxels.**
- **The separation of effects in the nearby medial and lateral orbitofrontal cortex was made possible by this voxel-level analysis.**

Cheng, Rolls et al 2016 Brain

Stop-signal task





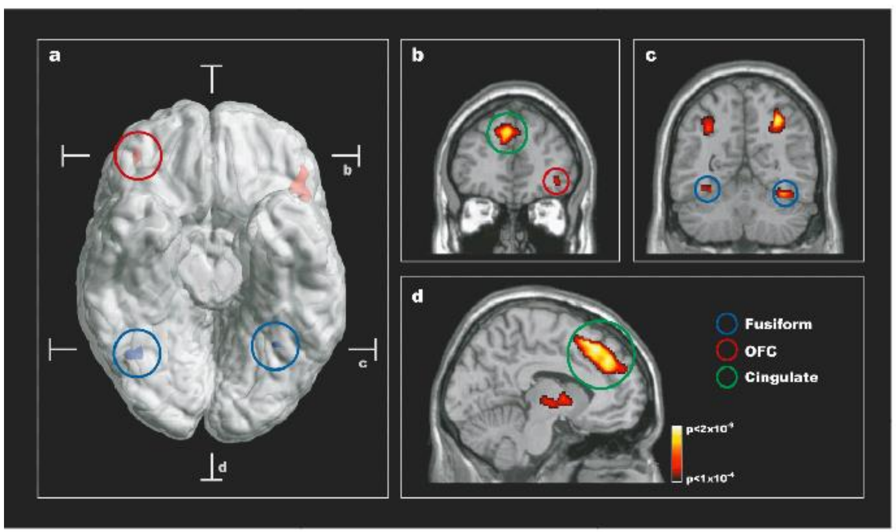
Activations in the human lateral orbitofrontal cortex are related to a signal to change behavior in the stop-signal task.

Deng, Rolls …, Robbins, Imagen, Schumann 2017 Human Brain Mapping. (1709 participants)

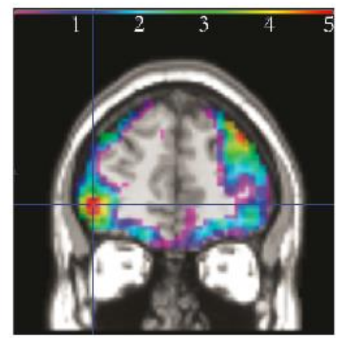
A non-reward attractor theory of depression

- a. Activation of the human lateral orbitofrontal cortex in a visual discrimination face emotion reversal task on reversal trials (Kringelbach and Rolls, 2003).
- b. Activations in the human lateral orbitofrontal cortex are related to a signal to change behavior in the stop-signal task (Deng, Rolls …, Robbins, Imagen, Schumann 2017 Human Brain Mapping. (1709 participants)
- Impulsive behavior is impaired by damage to the inferior frontal gyrus (Robbins)
- c. Bold signal in the macaque lateral orbitofrontal related to win-stay / lose-shift performance, that is, to reward reversal performance. (Chau, …Rushworth 2015 Neuron)

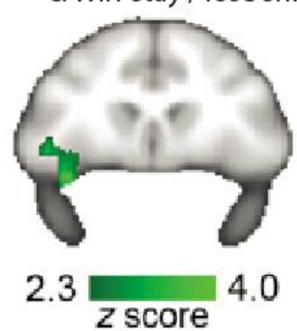
a. Reversal



b. Stop-signal task



c. Win-stay / lose shift



Rolls 2016 Neuroscience and Biobehavioral Reviews

Neuroeconomics:
Expected value; and value outcome

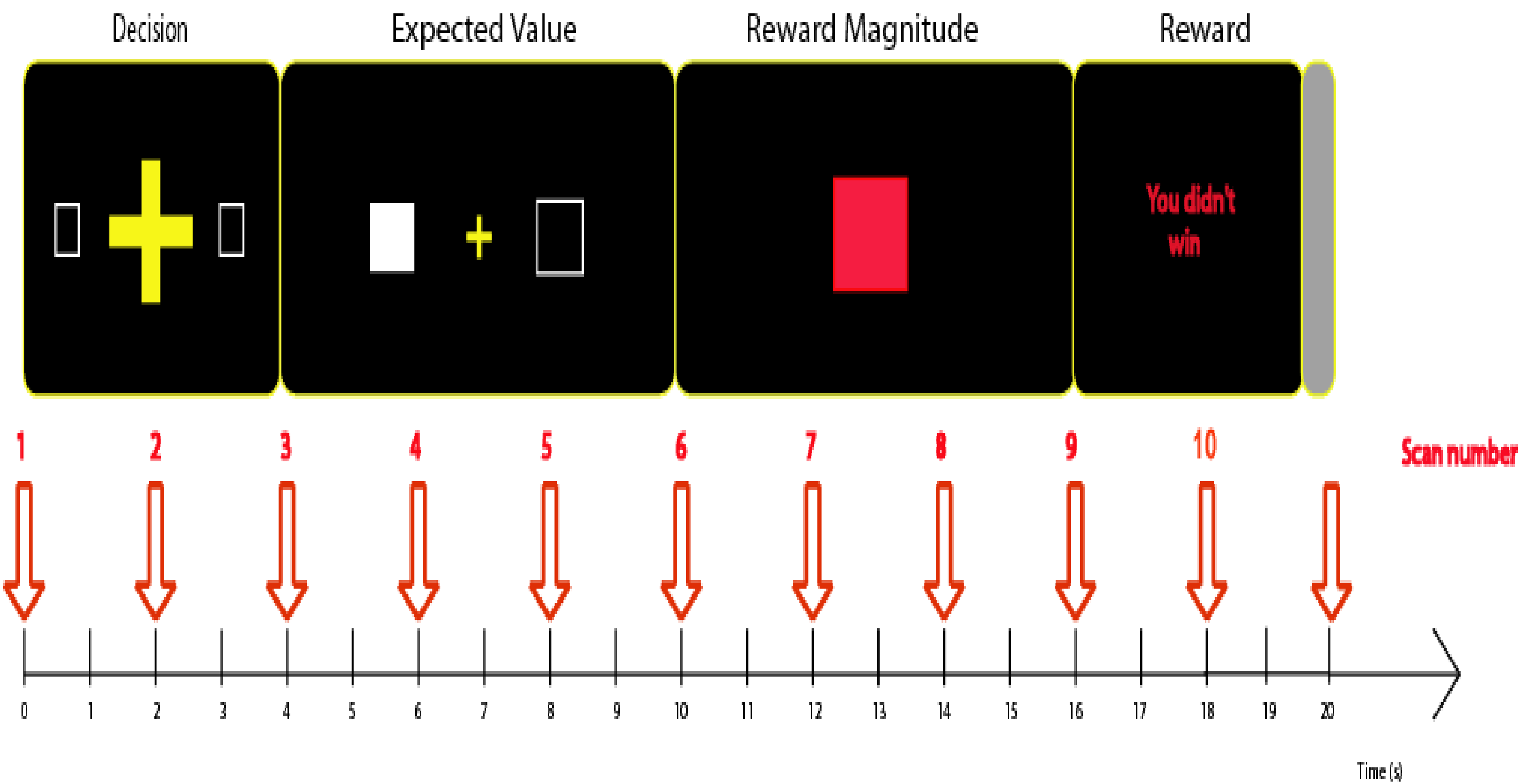
Expected Value = probability x Reward Magnitude

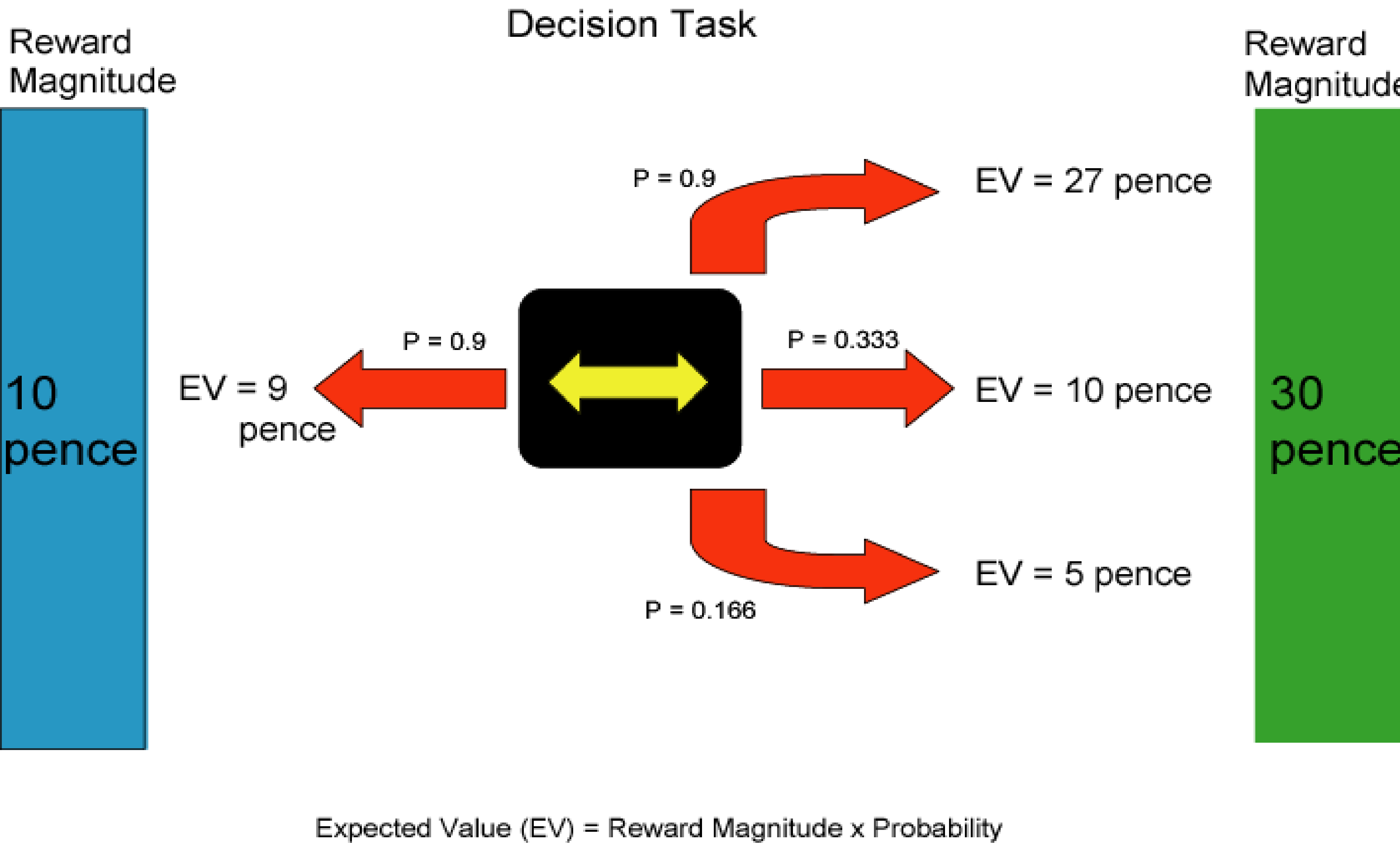
Expected utility ≈ Expected Value

Reward Prediction Error = Reward Magnitude – Expected Value

Rolls, McCabe and Redoute (2008) Cerebral Cortex 18

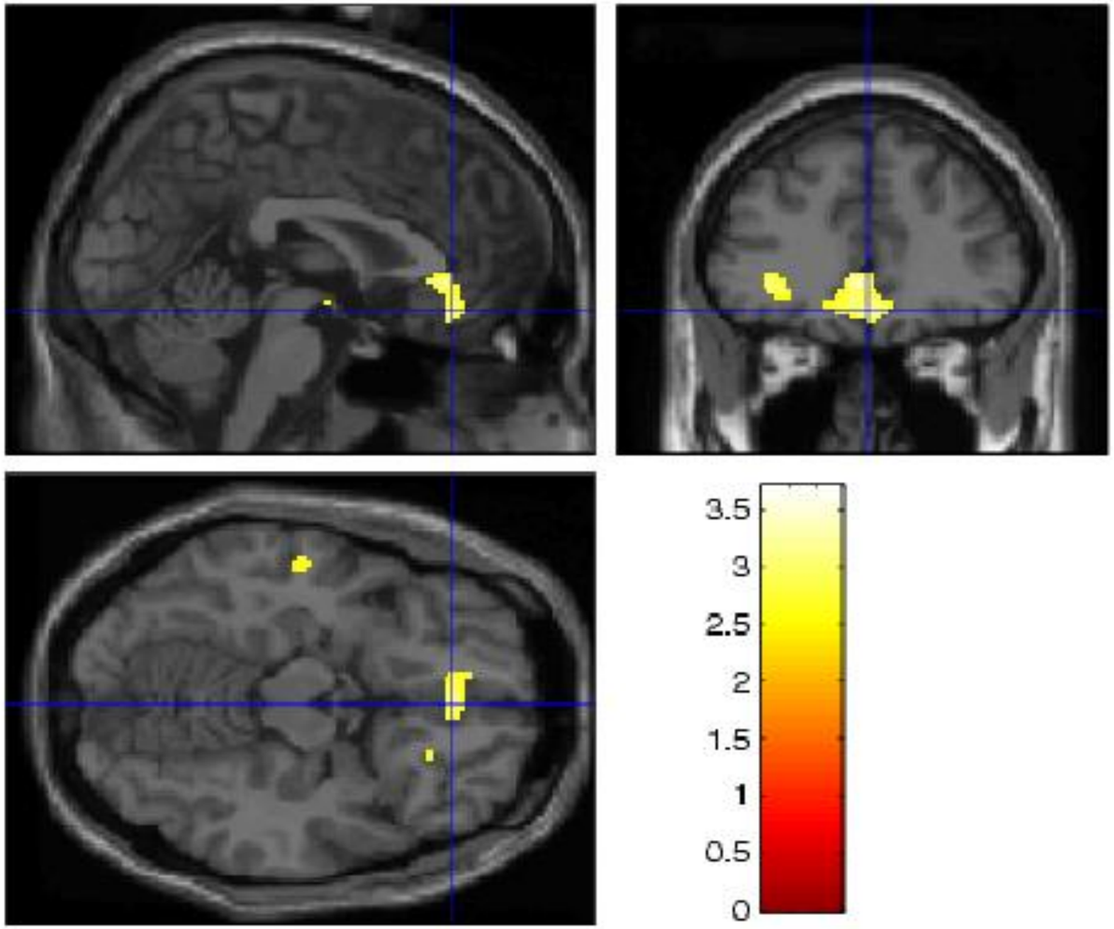
Scale diagram of 1 trial: scans and display





Rolls, McCabe and Redoute (2008) Cerebral Cortex 18

Medial orbitofrontal cortex / ACC: conjunction between Expected Value and Reward Magnitude



Rolls, McCabe and Redoute (2008) Cerebral Cortex 18

Neuroeconomics and classical economics

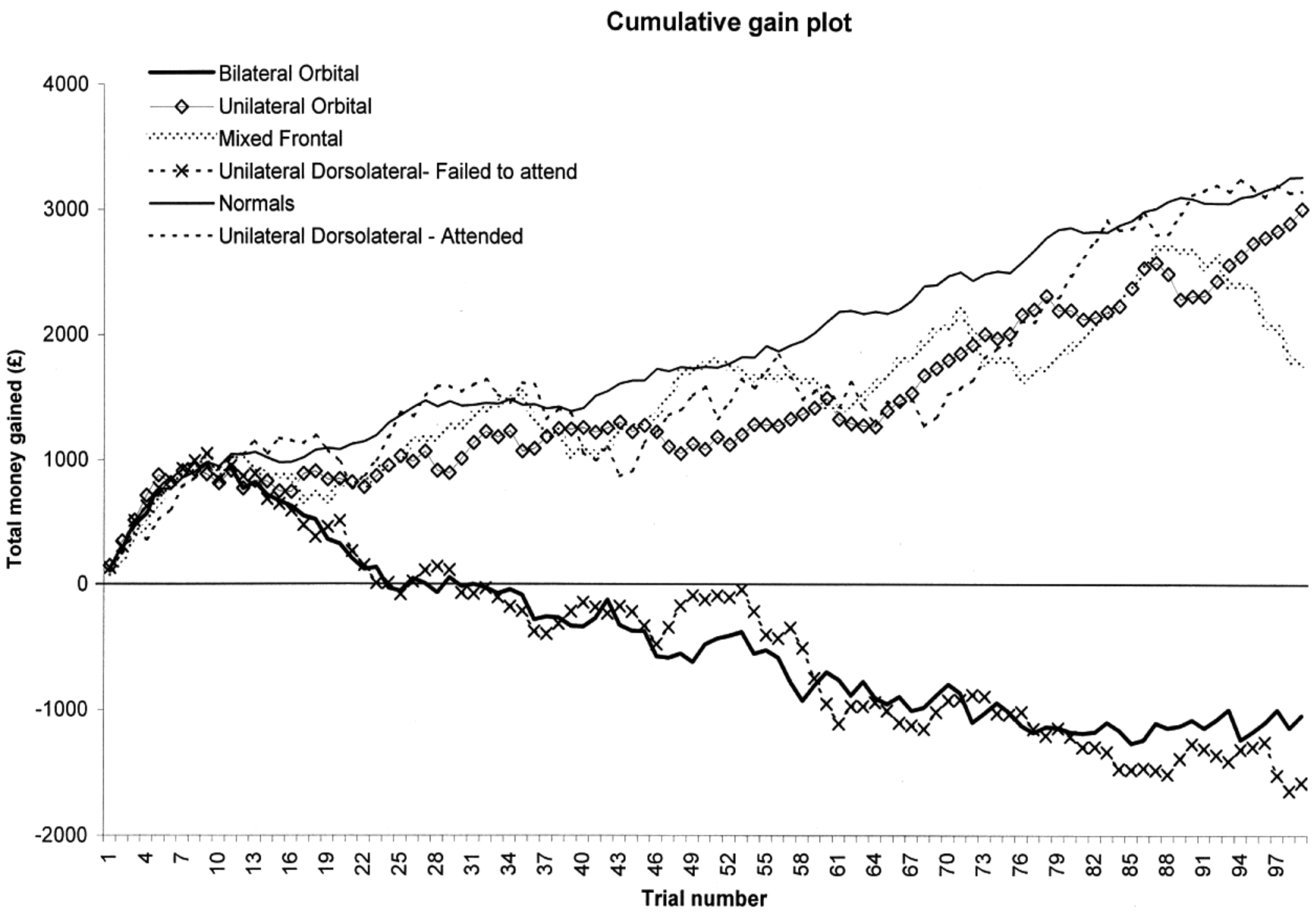
- **Classical economics assumes a few axioms, and rational, logical, application of those axioms.**
- **Neither may be correct.**
- **There may be multiple specific rewards that influence each decision.**
- **The decision-making may be produced by :**

  the emotional (short-term, with heuristics developed in evolution),

  or the rational (long-term, planning), system.
- **Which system is chosen, and the decision within each system, is subject to noise in the brain.**
- **Even in the rational system, logic may not be applied consistently well.**
- **Neuroeconomics may be able to identify many different value systems, and the probabilistic mechanisms used by the brain when making choices.**
- **Will neuroeconomics replace classical microeconomics?**

Rolls (2014) Emotion and Decision-Making Explained. Oxford.

Visual discrimination reversal task for monetary reward



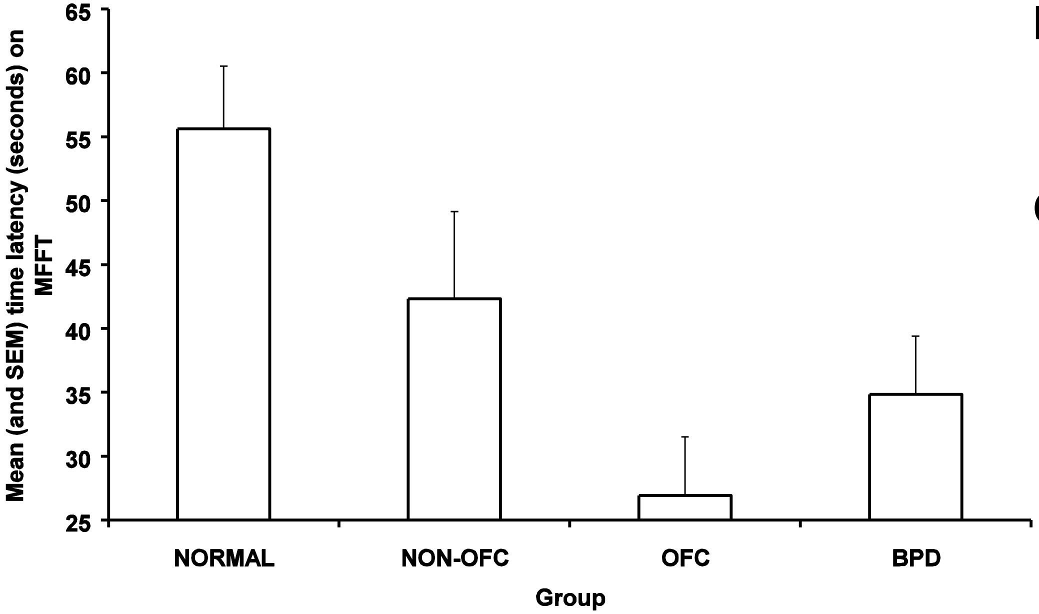
Bilat OFC

Dlpfc non-attenders

Patients with bilateral orbitofrontal cortex lesions lost money because they failed to reverse.

Some patients with dorsolateral prefrontal cortex lesions performed poorly because they failed to attend to the relevant feedback provided on each trial.

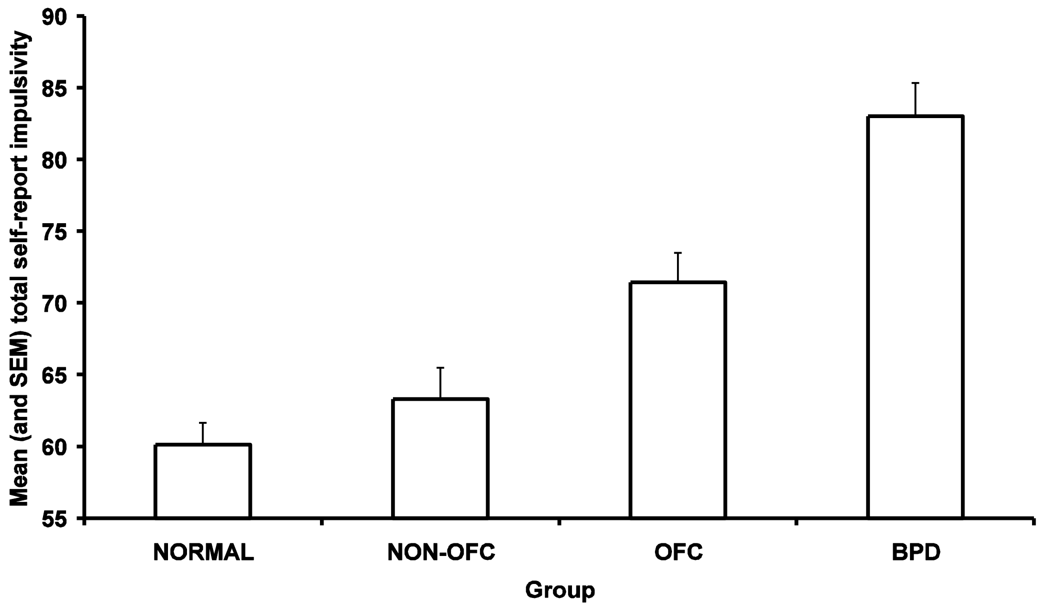
Behavioural impulsivity test: matching familiar figures



BPD – Borderline Personality Disorder (self-harmers)

OFC – OrbitoFrontal Cortex

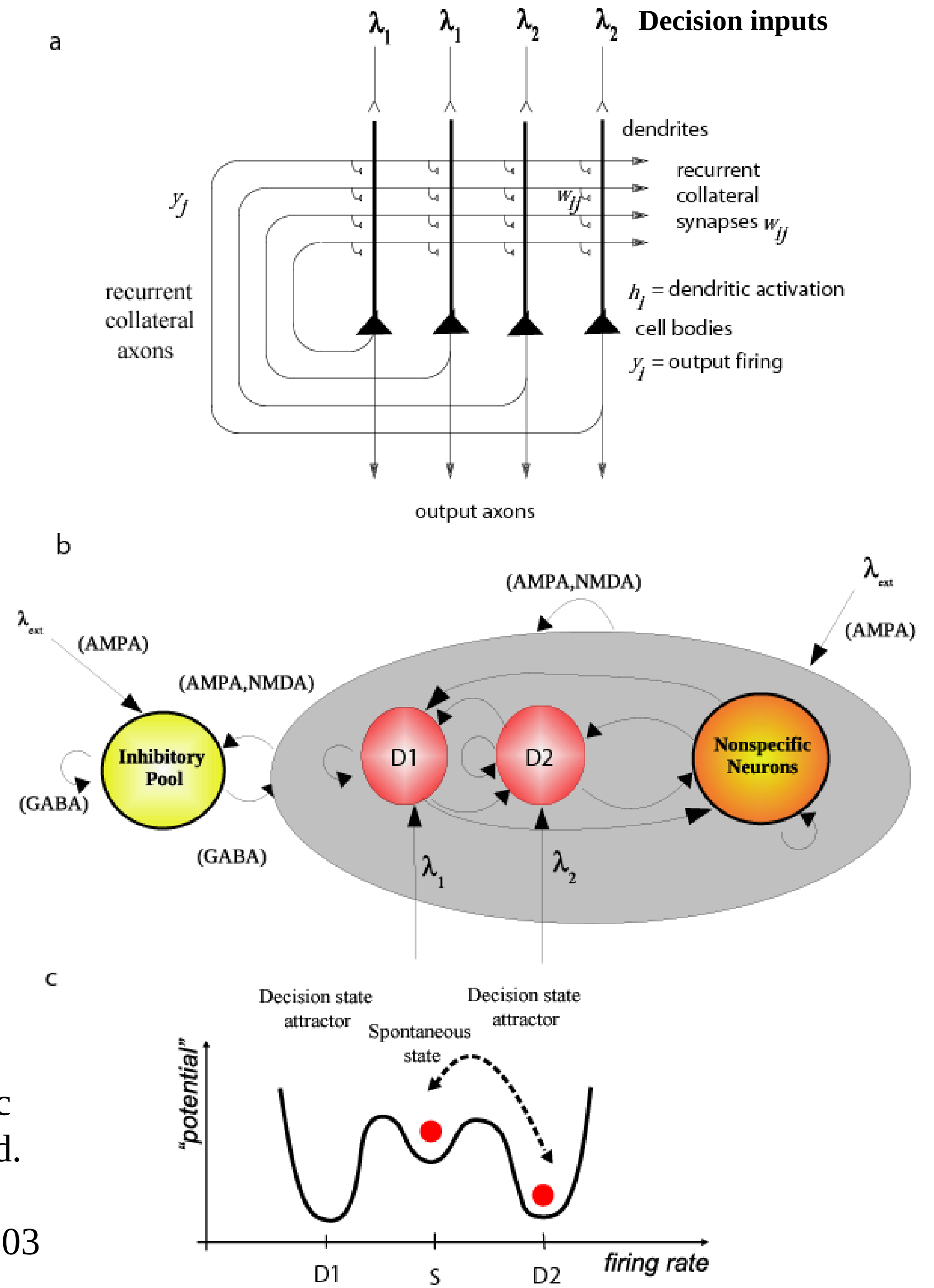
Self-report Impulsivity



Berlin,H., Rolls, E.T., and Kischka,U. (2004) Impulsivity, time perception, emotion, and reinforcement sensitivity in patients with orbitofrontal cortex lesions. Brain 127: 1108-1126.

An attractor network for probabilistic decision-making, with lambda 1 and 2 inputs, and noise from the neuronal spiking influencing which decision attractor, D1 or D2, wins.

This is also a model for short-term memory.



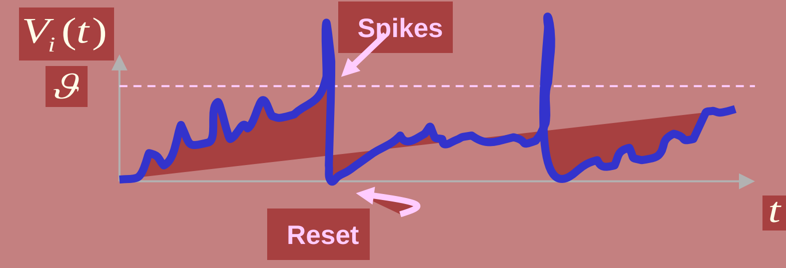
Brunel and Wang 2001.
Rolls and Deco 2010 The Noisy Brain: Stochastic Dynamics as a Principle of Brain Function. Oxford.

Deco, Rolls et al 2013 Progress in Neurobiology 103

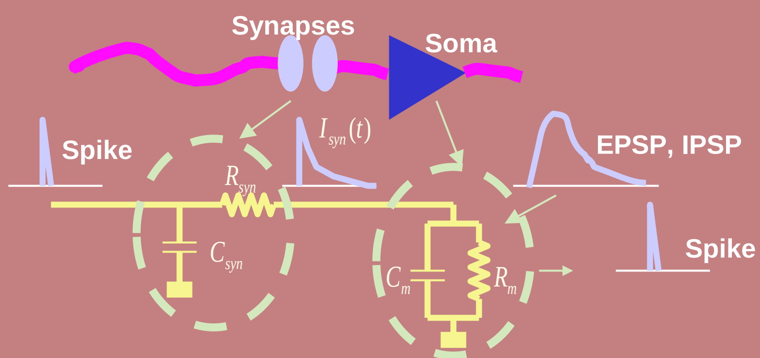
Neurodynamical Modeling: Neurons, Synapses & Cortical Architecture

Spiking Neuron -> Integrate-and-Fire Model:

$$\tau_m \frac{d}{dt} V_i(t) = -g_m (V_i(t) - V_L) - I_{syn}(t)$$



Synaptic Dynamics:

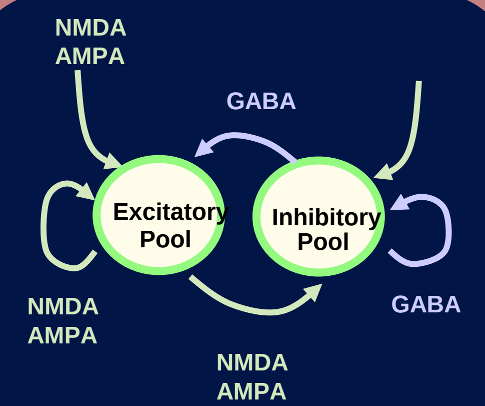


$$I\ (t) = g\ (V_i(t) - V_E)\, f(V_i(t)) \sum_j w_{ij} s_j(t)$$

$$\frac{d}{dt} s_j(t) = -\frac{s_j(t)}{\tau_{decay}} + \alpha x_j(t)(1 - s_j(t))$$

$$\frac{d}{dt} x_j(t) = -\frac{x_j(t)}{\tau_{rise}} + \sum_k \delta(t - t_j^k)$$

$$I_{syn}(t) = I_{AMPA,ext}(t) + I_{AMPA,rec}(t) + I_{NMDA,rec}(t) + I_{GABA,rec}(t)$$

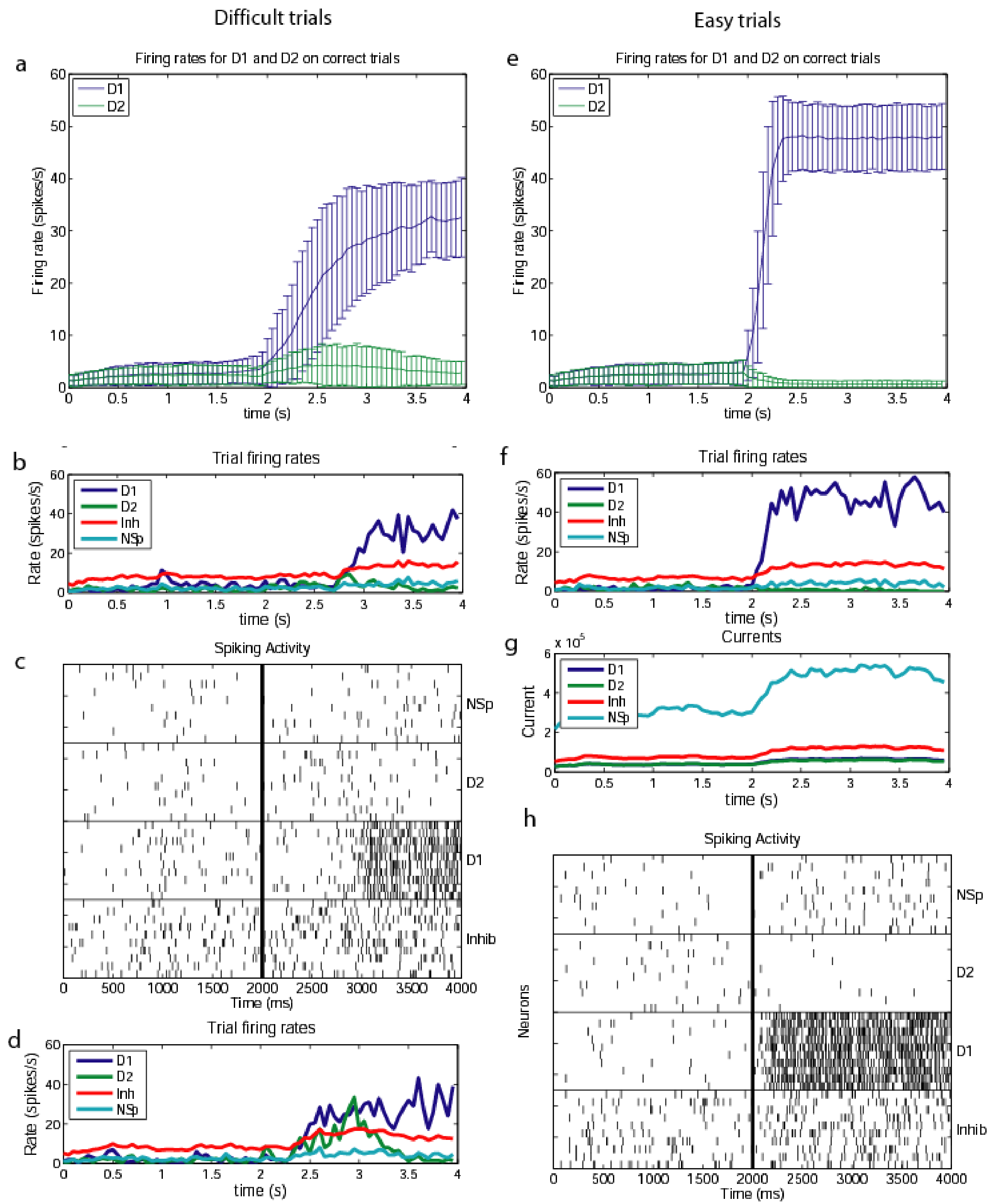


Dynamical Cooperation and Competition

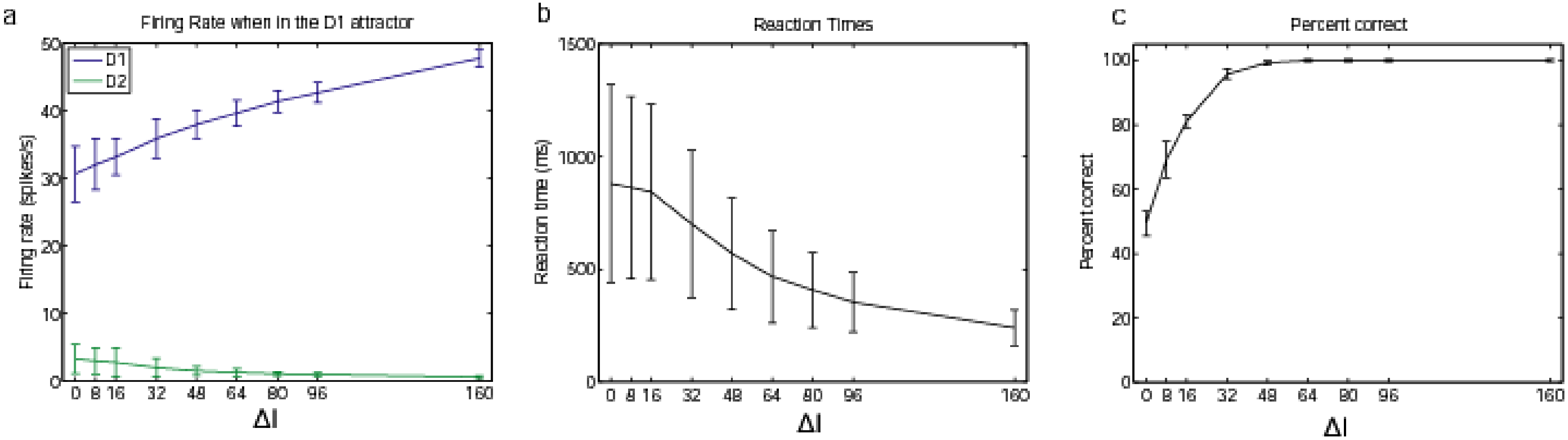
Integrate-and-fire simulations predict earlier and higher neuronal responses on easy vs difficult trials.

Confidence is reflected in the higher firing on easy trials.

The decision stimuli start at t=2 s

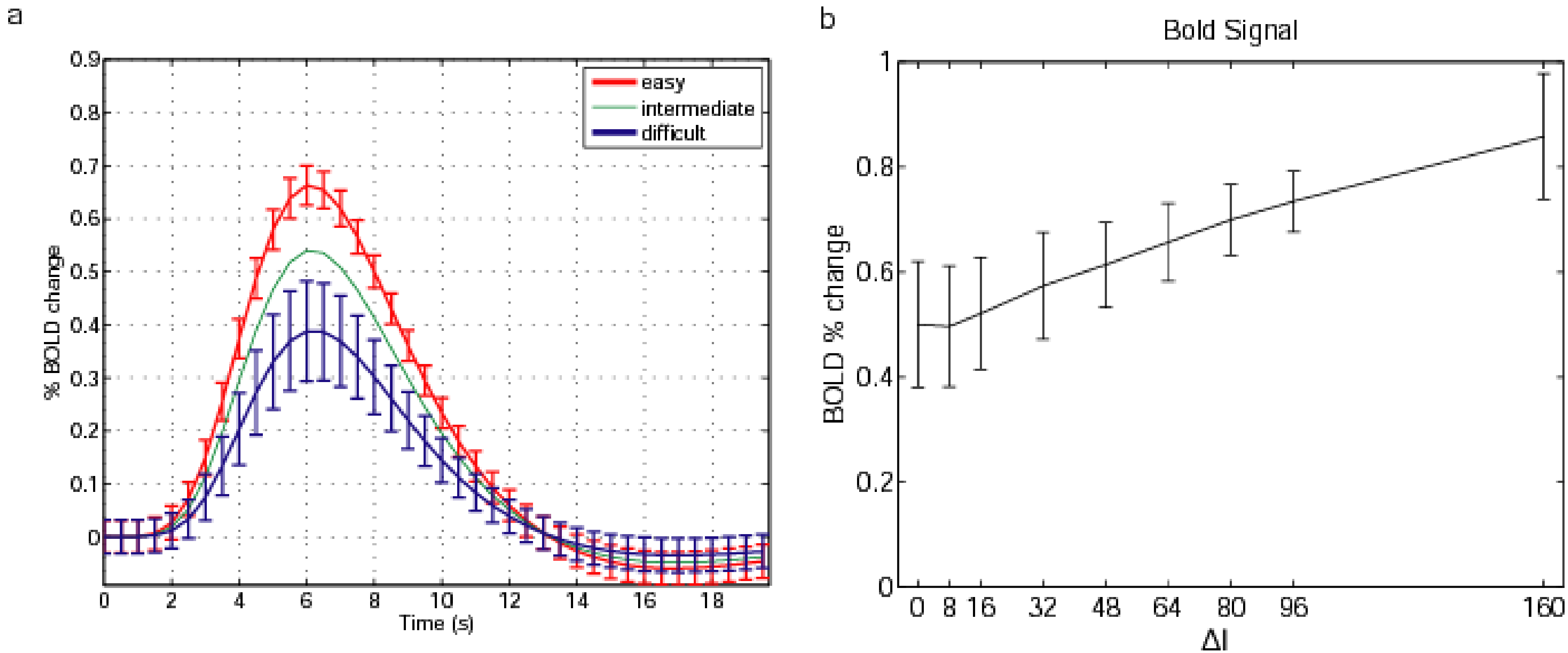


Rolls, Grabenhorst and Deco 2010 Neuroimage



- **The theoretical framework based in statistical mechanics predicts higher and faster neuronal responses as Delta I, the difference between the two stimuli, increases.**
- **Delta I is a measure of the easiness of the decision, and subjective confidence ratings correlate with this.**

Rolls, Grabenhorst and Deco 2010a Neuroimage



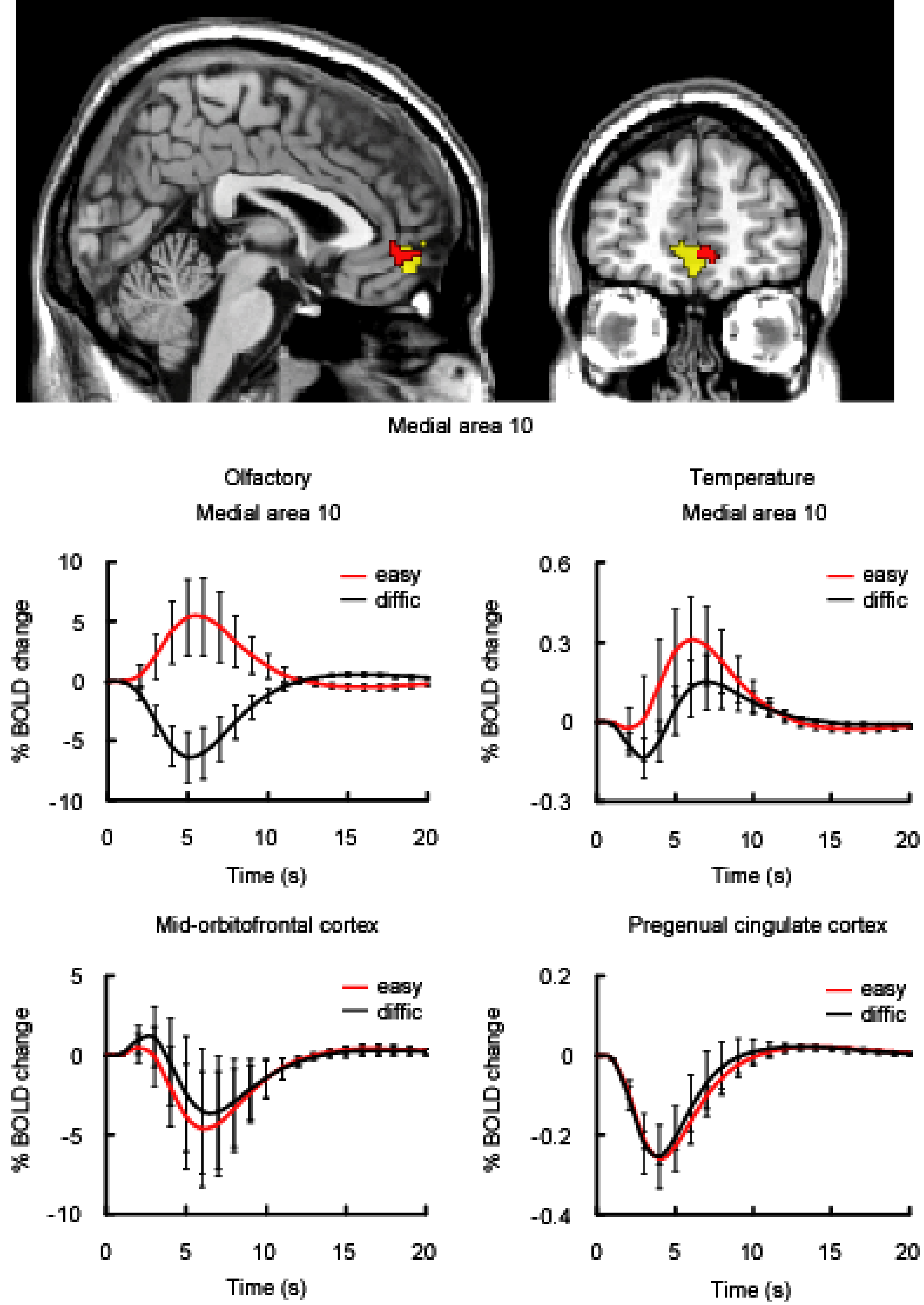
The theoretical framework therefore by convolution of the neuronal or synaptic activity with the haemodynamic response function predicts a larger BOLD response on easy vs difficult trials.

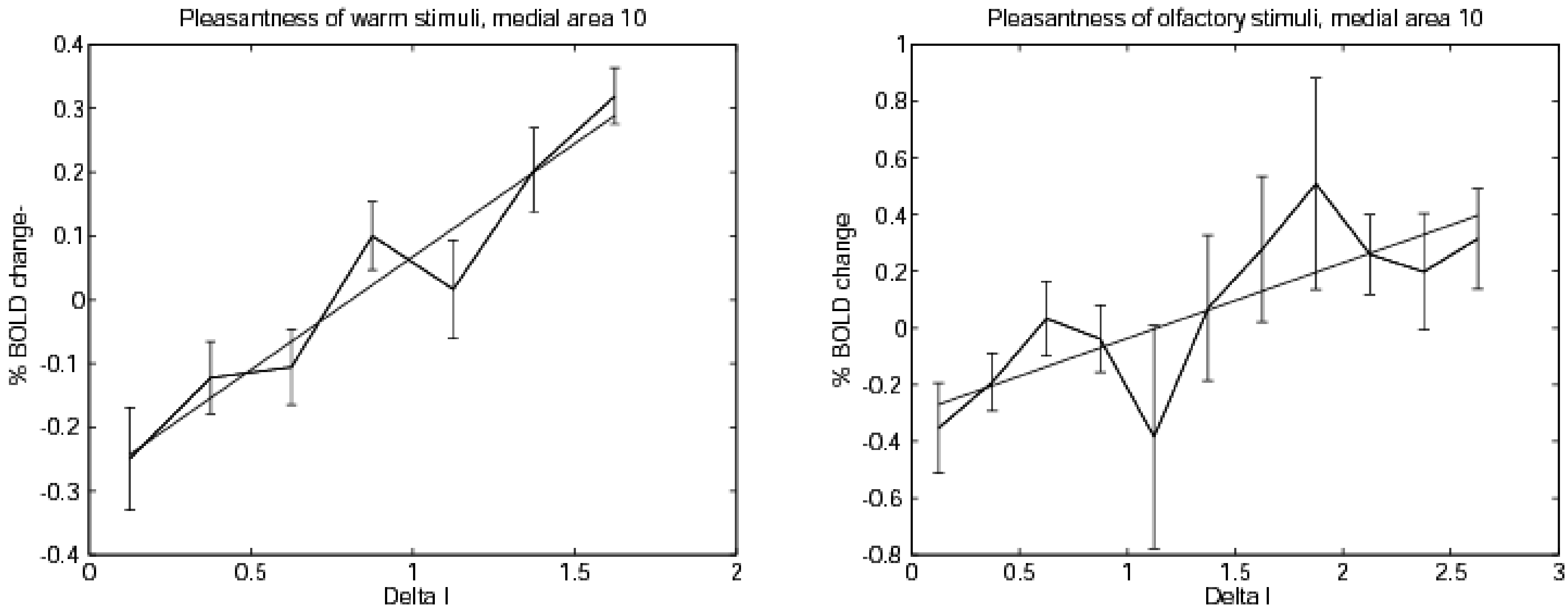
(Easy trials have large Delta I)

Rolls, Grabenhorst and Deco 2010 Neuroimage

- The Bold signal was, as predicted by the model, larger on easy vs difficult trials in medial prefrontal cortex area 10, implicated in decision-making; but not in mid-orbitofrontal cortex, implicated in a continuous representation of affective value
- Data from an olfactory and a thermal decision task

Rolls, Grabenhorst and Deco 2010 Neuroimage

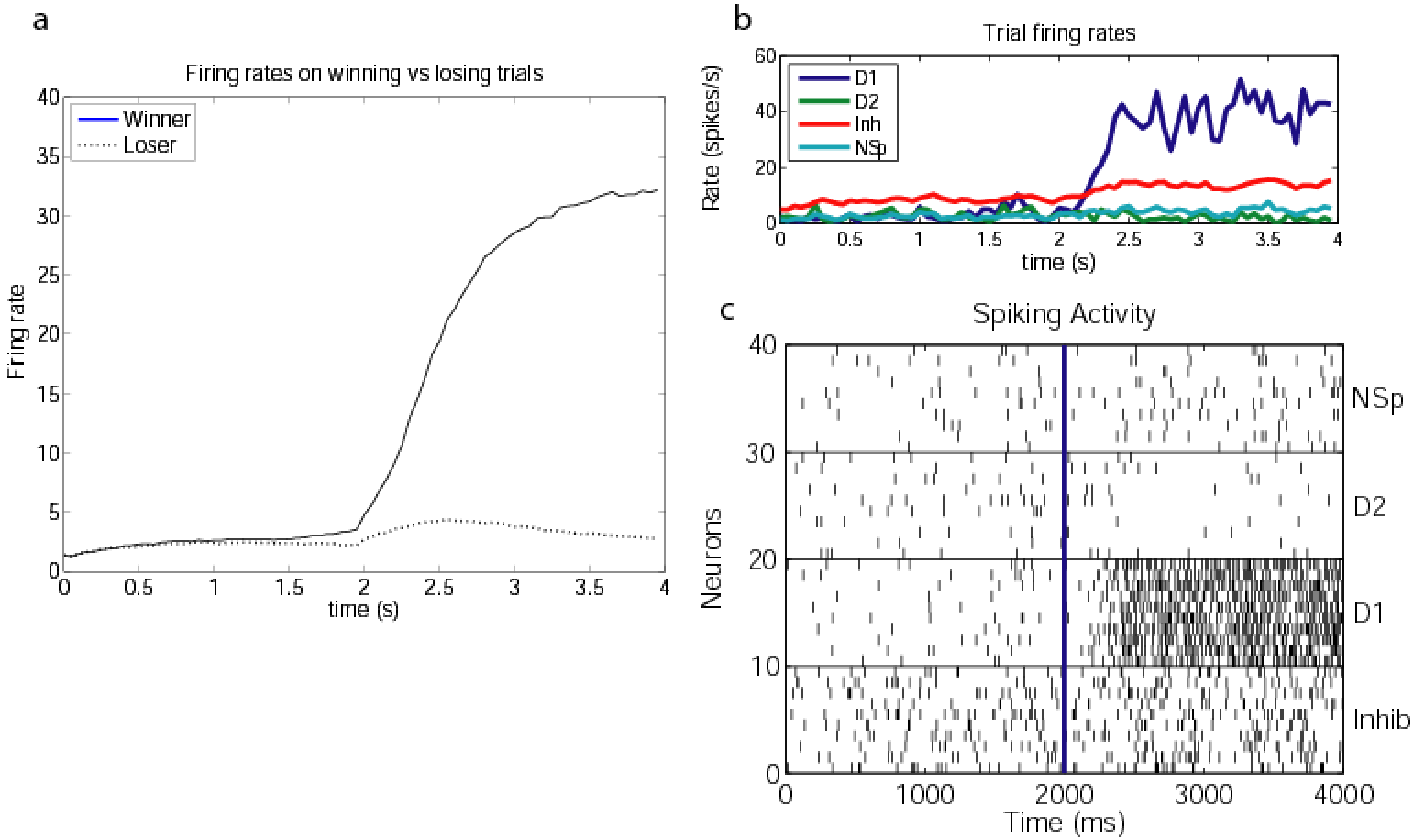




- **The BOLD signal was, as predicted by the model, larger on easy vs difficult trials in medial prefrontal cortex area 10, implicated in decision-making;**
- **but not in mid-orbitofrontal cortex, implicated in a continuous representation of affective value.**
- **Subjective, conscious, decision confidence is reflected in the firing rate of the winning attractor – an emergent property**

Rolls, Grabenhorst and Deco 2010 Neuroimage

Prediction of a decision at 70% correct, before the evidence is provided at t=2 s



Rolls and Deco (2010) The Noisy Brain. Oxford University Press
Rolls and Deco (2011) Frontiers in Neuroscience 5

Noise in the brain predicts decisions

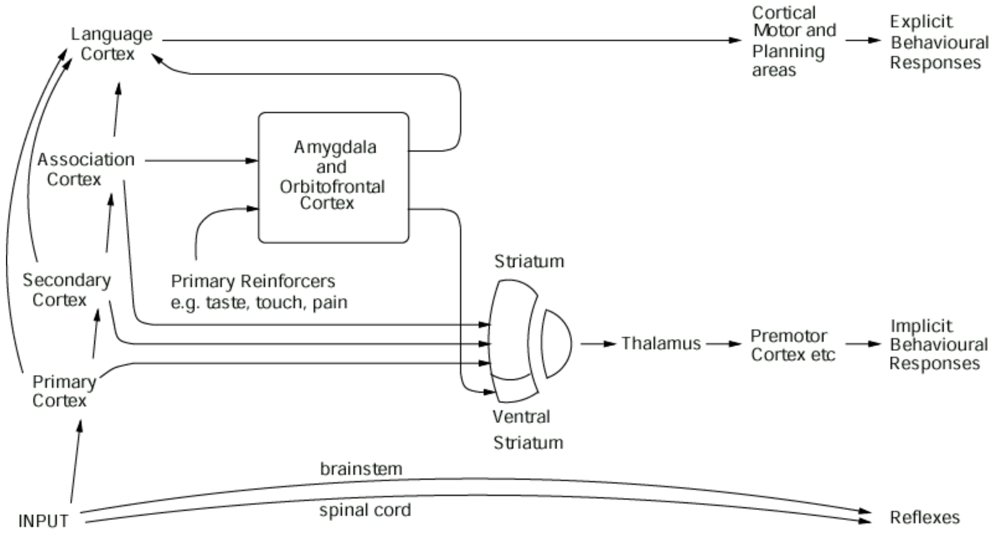
- Prediction of someone's decision from the noise in the brain before the evidence for the decision is even given.
- The noise arises from the statistical fluctuations produced by the nearly Poisson spike times (random for a given mean firing rate).
- What one reports as a conscious decision, reflecting one's free will, can be predicted from noise in the brain.

- Where does that leave free will?

Rolls and Deco (2010) The Noisy Brain. Oxford University Press
Rolls and Deco (2011) Frontiers in Neuroscience 5

Consciousness, free will, and The Noisy Brain

- **The rational, reasoning, system allows gene-specified rewards not to be chosen, in the long-term interests of the individual, the phenotype.**
- **Noise influences choices between genes vs the phenotype.**
- **Confabulation: if noise makes us choose based on implicit brain systems, we nevertheless report consciously that we took the decision, and may provide a spurious, confabulated, reason or explanation for our decision.**
- **In this case I propose that conscious free will reports reflect an illusion: the free will in these cases is an illusion.**
- **So let us reserve free will for when the rational, Conscious, system has taken the decision.**
- **Confabulation may be adaptive: it allows the rational, reasoning, system to maintain consistency and continuity of the conscious self.**



Rational (reasoning) system

The emotional system

Principles of brain organization for decision-making (1)

1. The identity and intensity of stimuli are computed first in cortical processing – 'what" representations. Tier 1.

This enables us to identify and learn about stimuli independently of whether we currently want them and find them rewarding and affective

2. Reward value and pleasure are represented on a continuous scale in the orbitofrontal cortex (OFC) in terms of stimulus value, and also in the anterior cingulate cortex as an input to an action-goal outcome learning system. Tier 2.

This is a suitable representation as an input to decision-making systems

3. Many different rewards are represented close together in OFC and ACC, including taste, olfactory, oral texture, temperature, touch, visual, social, amphetamine-induced, and monetary rewards.

This facilitates comparison and common scaling of different rewards by lateral inhibition, and thus provides appropriately scaled inputs for a choice decision-making process.

4. Spatially separate representations of pleasant stimuli (rewards) in medial OFC and pregenual ACC and unpleasant stimuli (punishers) in lateral OFC and dorsal ACC.

This provides separate and partly independent inputs into brain systems for cost-benefit analysis and decision-making.

5. The value of specific rewards is represented in OFC: different single neurons respond to different combinations of specific taste, olfactory, fat texture, oral viscosity, visual, and face and vocal expression rewards.

This provides for selection of specific rewards, but also for sensory-specific satiety. Specific goals must be provided for actions, as the actions for different goals are different.

A common scale of different rewards, but not a common currency.

6. Both absolute and relative value signals are represented in OFC.

Absolute value is necessary for stable long-term preferences and economic transitivity.

Relative value is useful in optimizing sensitivity to local reward gradients (e.g. positive contrast effects).

7. Top-down cognitive and attentional factors, originating in lateral prefrontal cortex, modulate reward value and pleasantness in OFC and ACC through biased activation.

These top-down effects allow cognition and attention to modulate the first cortical stage of reward processing to influence valuation and economic decision-making.

Rolls (2014) Emotion and Decision-Making Explained (OUP) . Grabenhorst and Rolls 2011 TICS. Rolls (2016) Cerebral Cortex (OUP)

Principles of brain organization for decision-making (2)

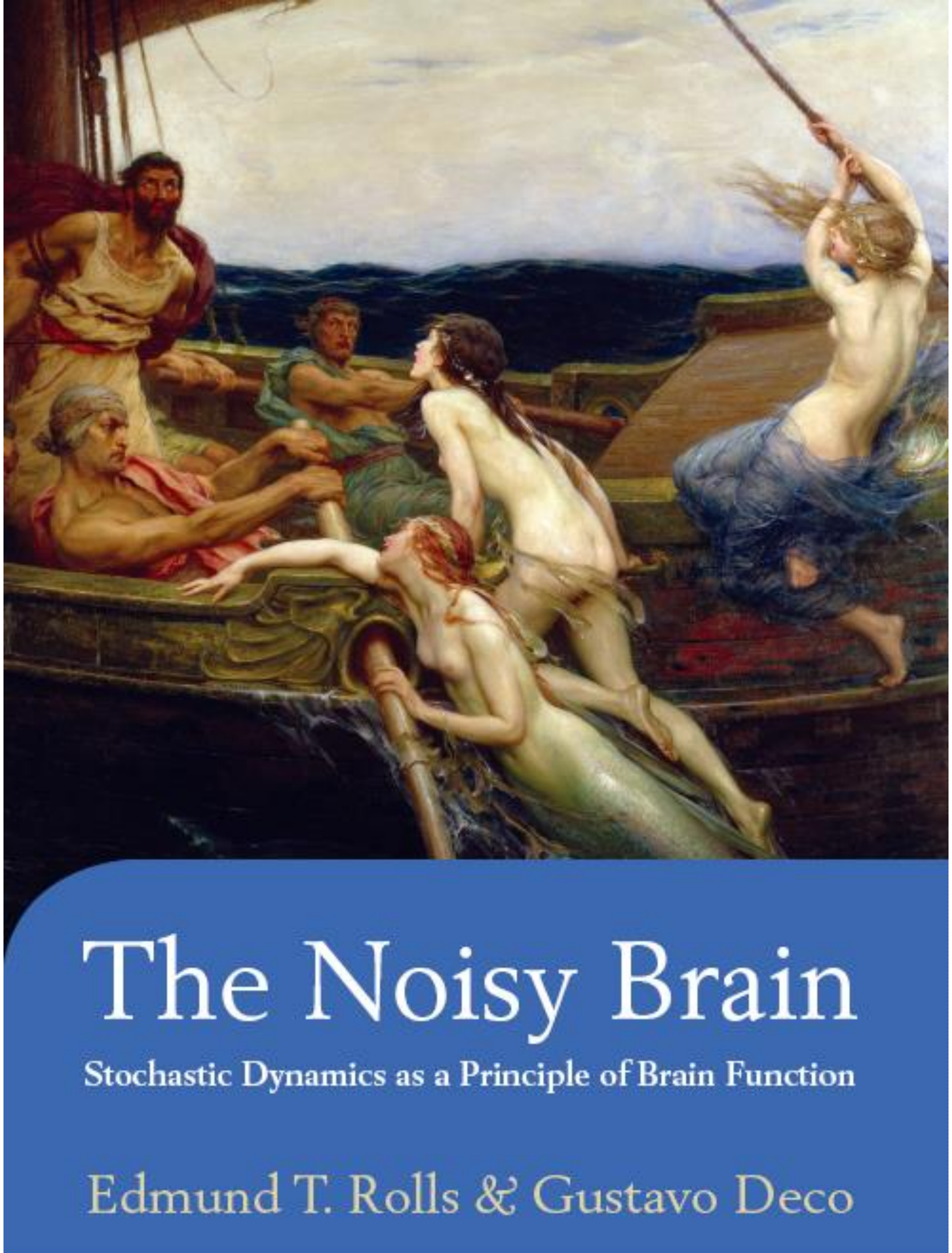
8. Choice decisions involve categorization and are made in a third tier.
   For choices between values this is the medial prefrontal cortex area 10, just anterior to OFC.
   We can simultaneously represent the value on a continuous scale (in OFC),
   and the categorical choice made on an individual trial (in MA10).
9. The choices are made by competition to produce a single winner in an attractor network with separate attractors each biased by the separate continuous inputs.
   This enables the decision state to be maintained in time as a short-term memory to provide the specific goal for action.
10. The decision-making is probabilistic because of the noise introduced by the (Poisson) randomness in the spike timing of neurons, which influences stochastically which attractor wins on a particular trial.
    This facilitates choosing less favourable options sometimes as in the matching law in which choice probability reflects reward value; unpredictable behaviour; memory recall which is non-deterministic and therefore allows creativity.
11. Confidence is an emergent property of the decision mechanism
12. 'Monitoring' can be performed by a second decision-making network.
13. The same noise-influenced decision-making (choice, categorization) process and the stability of the stochastic dynamics provides a unifying approach to:
    - decision-making in other systems, e.g.
      - optic flow in the parietal cortex (Shadlen)
      - vibrotactile flutter frequency decision-making in the ventral premotor cortex (Romo)
      - between the emotional and rational (reasoning) systems
    - memory recall
    - short-term memory and therefore top-down attention
    - creativity in thought processes (as a noise influenced trajectory through a state space of associatively linked representations; also dreams)
    - signal detection (as in stochastic resonance)
    - stochastic dynamics and free will
    - unpredictable responses (which can be evolutionarily adaptive)
    - schizophrenia (as reduced stability of the high and low firing rate states in cognitive systems in the face of noise)
    - aging (as reduced stability of high firing rate states in cognitive systems in the face of noise)
    - obsessive-compulsive disorder (as increased stability of high firing rate states in the face of noise)

Rolls (2014) Emotion and Decision-Making Explained (OUP) . Grabenhorst and Rolls 2011 TICS. Rolls (2016) Cerebral Cortex (OUP)

Principles of brain organization for economic decision-making (3)

1. Decisions are made by non-linear attractor neural networks in the brain, with noise produced by the random spiking times of neurons.
2. For this reason decision-making is probabilistic. Decision should be taken several times.
3. There are two ways of making decisions:
   - reward / emotion-based heuristics (habit; goal-directed; one trial reversal).
   - the reasoning system.
4. The interests of these two systems are different:
   - the reward / emotional system has genetic interests
   - the rational / reasoning / language-based system can be influenced by the interests of the phenotype.
5. Who chooses between these systems?
   - another noisy decision-making process in the brain
   - and the rational system may confabulate
6. Even the rational system does not meet the criteria of microeconomics
   - its logic and weighting of outcomes is imperfect
   - it is noisy / probabilistic
7. There are many different rewards, many set as goals by genes.
   - A common scale, but no common currency
   - There are many heuristics, not a few axioms.
   - There are individual differences in the reward weightings in different individuals.
   - Sensitivity to non-reward also differs between individuals, reflected in impulsiveness.
   - In depression, there is an overactive non-reward system, and reduced impulsiveness.
   - The opposite may be true in the manic phase of bipolar disorder.

Rolls (2014) Emotion and Decision-Making Explained (Oxford University Press) . Rolls (2016) Cerebral Cortex (Oxford University Press)



www.oxcns.org

Emotion and Decision-Making Explained. 2014

The Brain, Emotion, and Depression. 2018

Oxford University Press 2010

Advantages of noise in the brain

1. Choices are made by competition to produce a single winner in an attractor network with separate attractors each biased by the separate continuous inputs.

The decision-making is probabilistic because of the noise introduced by the (Poisson) randomness in the spike timing of neurons, which influences stochastically which attractor wins on a particular trial.

This facilitates choosing less favourable options sometimes as in the matching law in which choice probability reflects reward value. This is adaptive, as the environment may change. Foraging...

2. Unpredictable behaviour: useful in predator avoidance, and in games. Can be evolutionarily adaptive.

3. Memory recall, the same process, is non-deterministic, and this allows creativity.

Creativity in thought processes (as a noise influenced trajectory through a state space of associatively linked representations; also dreams)

4. Individual differences in noise may enable creativity with its dangers such as schizophrenia;

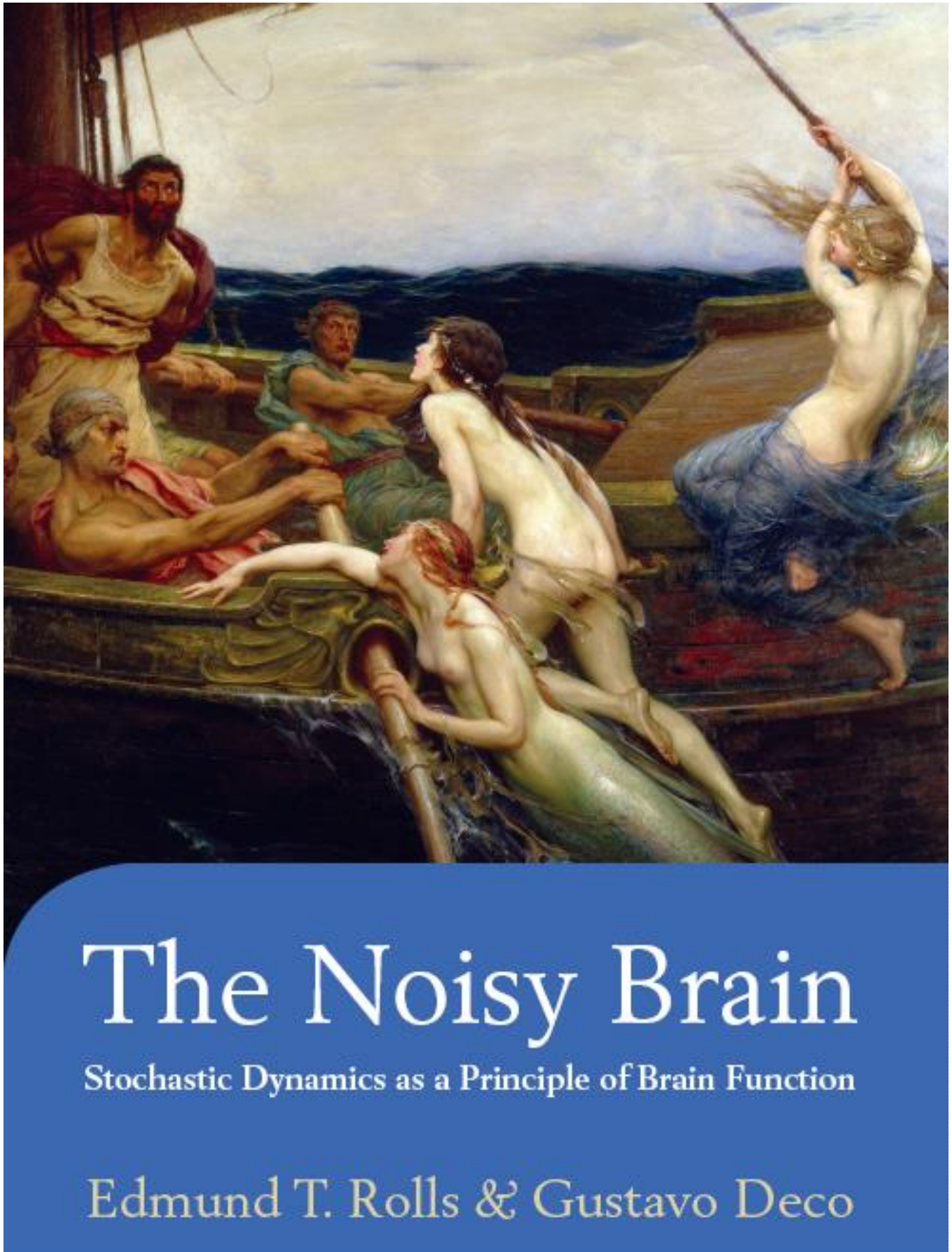
vs greater stability of thought, focussing of attention on goals, with its dangers such as obsessive-compulsive disorder.

5. Decision-making between the emotional and rational (reasoning) systems.

6. Short-term memory is variable, with noise fluctuations freeing the short-term memory for further items.

7. Signal detection close to threshold (as in stochastic resonance).

Rolls and Deco (2010) The Noisy Brain (Oxford University Press)
Rolls (2012) Neuroculture (Oxford University Press)
Rolls (2016) Cerebral Cortex (Oxford University Press)



Oxford University Press 2010

www.oxcns.org

Neuroeconomics and reward systems in the brain

1. Value representations of many different reinforcers in the orbitofrontal cortex.
2. The value of each reinforcer must be scaled by natural selection on a common scale that promotes choosing of each reinforcer sometimes, in the interests of fitness (reproductive success by individual genes, which must cooperate as well as compete).
3. However, natural selection involves genetic variation, and therefore the profile of reinforcers will be different in different individuals.
4. Thus a few axioms applied logically to the rational decision-maker (classical microeconomics) will not do.
5. Instead, we must develop an understanding of value systems that are specific for different types of value, different in different individuals, and often influence behaviour by heuristics not by rational calculation.
6. Humans in any case are often poor at calculation of expected value (rewards and costs in probabilistic decision-making).
7. Animals (including humans) will be very sensitive to expected losses (e.g. injury, wealth and resources, reputation), as a single loss could impair reproductive success.
8. Noise in the brain can influence decision-making.
9. Humans have two ways of making decisions:
    1. The emotional system optimising gene-specified reinforcers in the interests of the ‘selfish’ genes.
    2. The rational system optimising reinforcers in the interests of the ‘selfish’ individual.
    3. Noise in the brain may influence even the decisions between these two systems.
10. Will neuroeconomics replace classical microeconomics?

Rolls 2014 Emotion and Decision-Making Explained. Oxford University Press

Brain systems for changing and stopping behaviour

1) The emotional vs the reasoning brain systems: who chooses between them?
2) Stochastic decision-making by attractor networks is part of the mechanism.
3) The medial orbitofrontal cortex (medOFC) represents reward value, which is likely to be involved.
4) Top-down cognition is a major factor in modulating the reward value in the medOFC, and is likely to be involved.
5) The lateral orbitofrontal cortex represents punishers, and computes non-reward (in that an attractor network becomes active when an expected reward is not obtained), both of which normally change behaviour.
6) The lateral orbitofrontal cortex also is required for stopping behaviour (in the SSRT).
7) Damage to the orbitofrontal cortex impairs behavioural changes to non-reward, and makes people impulsive.
8) Depression may involve over-reactivity of the lateral orbitofrontal cortex to non-reward.
9) Tribalism as an evolutionary adaptation, that encourages some individuals to commit their agency to that of the group, so that what is done is almost automatic, and is justified by allegiance to the in-group, to the tribe. Some individuals may resist their agency being taken over in this way, and may think through each decision with their reasoning system. The engagement of this reasoning system may be an antidote to handing over one’s sense of agency to the in-group. Perhaps holding each individual responsible for their actions performed using reasoning would help: the rational actor.

Functional connectivity in depression

- The first brain-wide voxel-level resting state functional-connectivity neuroimaging analysis of depression.
- Big data, and multicenter collaboration, with 421 patients with major depressive disorder and 488 controls, were used to obtain statistically significant measures of voxel-level functional connectivity.
- Resting state functional connectivity between different voxels reflects correlations of activity between those voxels, and is a fundamental tool in helping to understand the brain regions with altered connectivity and function in depression.
- Each resting-state fMRI image included 47,619 voxels. For each pair of voxels, the time series were extracted and their correlation was calculated for each subject. Two-tailed, two-sample t-tests were performed on the 1,133,760,771 (47619×47618/2) functional connectivities between every pair of voxels.
- For the functional connectivity of a voxel to be treated as significantly different (p<0.01) after FDR correction from another voxel, the significance level uncorrected had to be $\mathrm{p} < 2.52 \times 10^{-7}$.

Cheng, Rolls et al 2016 Brain

Functional connectivity in depression

- Wei Cheng[1], Edmund T. Rolls[2,3]; Jiang Qiu[4,5]; Wei Liu[4,5]; Yanqing Tang[6]; Chu-Chung Huang[7]; XinFa Wang[8,9,10]; Jie Zhang[1]; Wei Lin[1]; Lirong Zheng[14,15]; JunCai Pu[8,9,10]; Shih-Jen Tsai[11]; Albert C Yang[11]; Ching-Po Lin[7]; Fei Wang[6]; Peng Xie[8,9,10]; Jianfeng Feng[1, 2, 12, 13]

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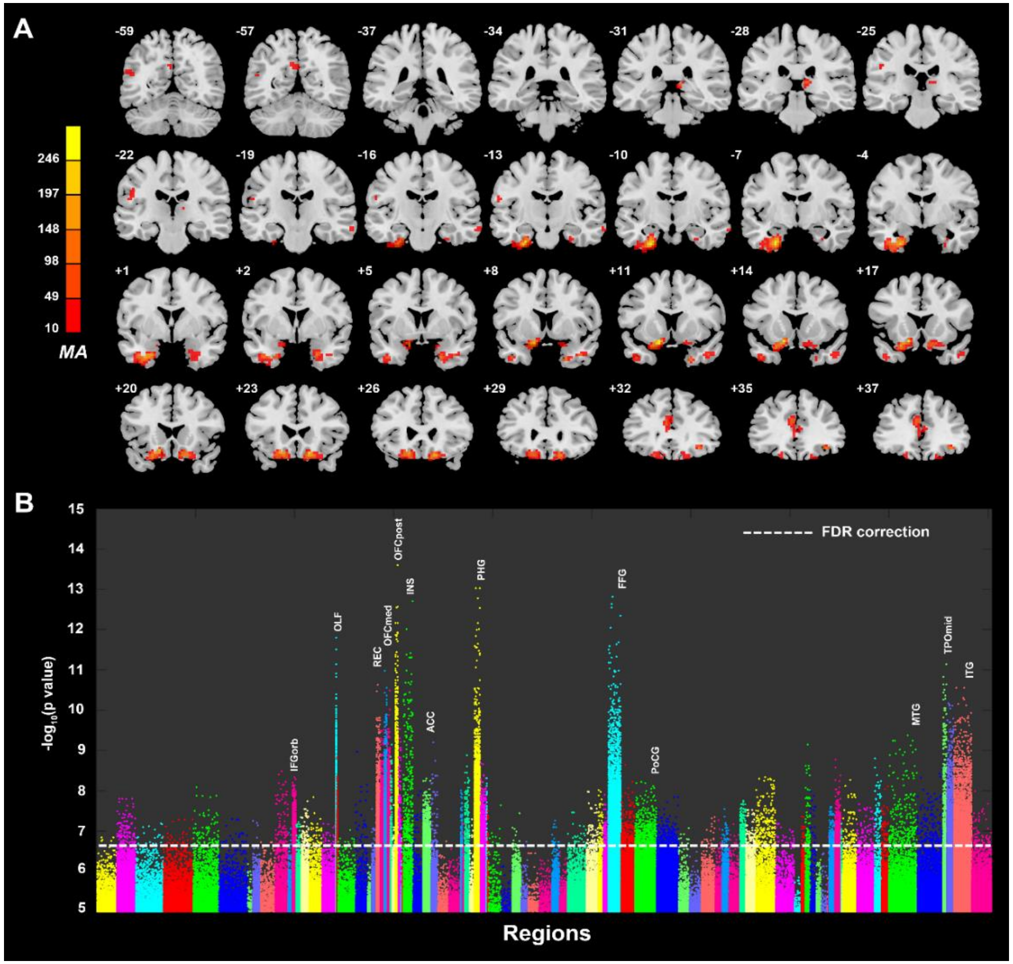
- 15. KTH - Royal Institute of Technology, Sweden.

Cheng, Rolls et al 2016 Brain

Functional connectivity in depression

- Voxels in the medial and lateral orbitofrontal cortex, parahippocampal cortex, and precuneus with significantly different functional connectivity in depression.



- P values of voxels in different brain regions. The horizontal line shows the significance level after FDR correction.

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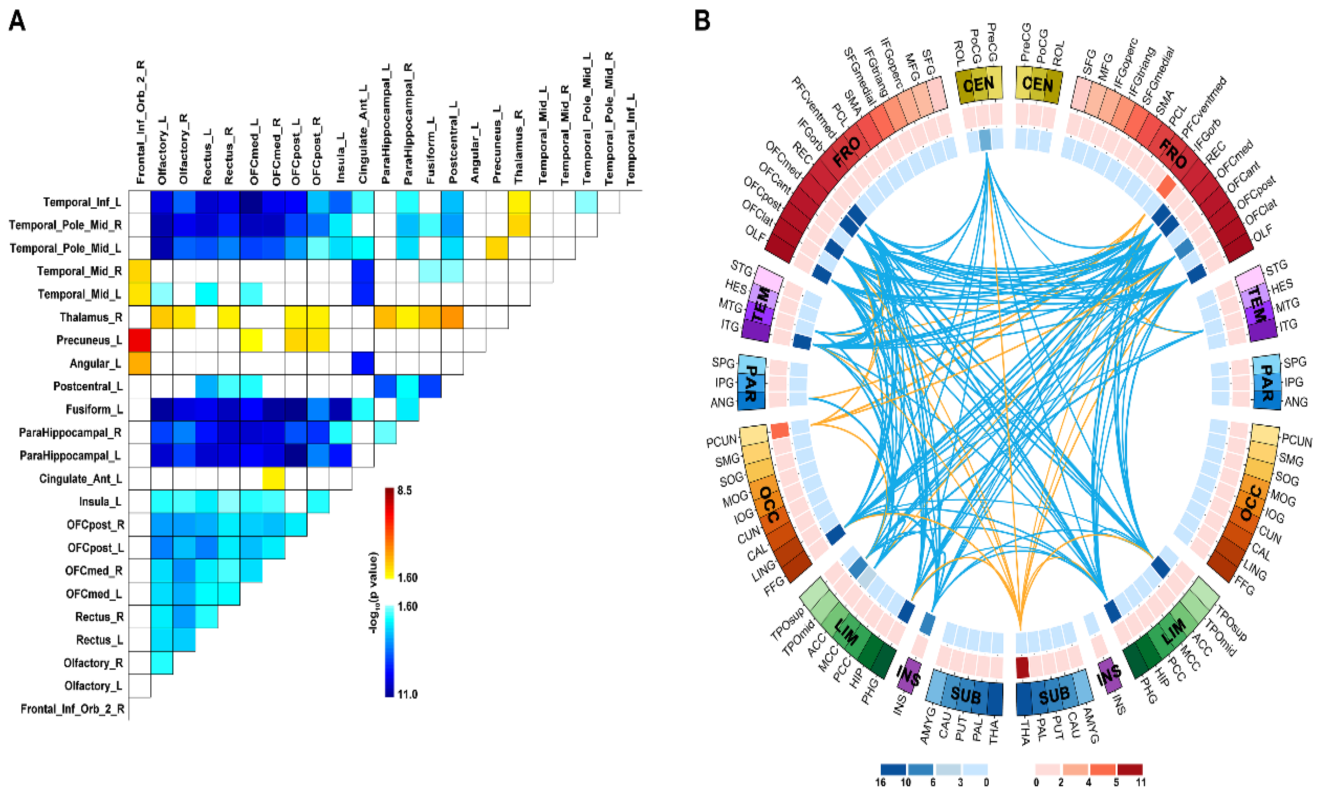
Functional connectivity in depression

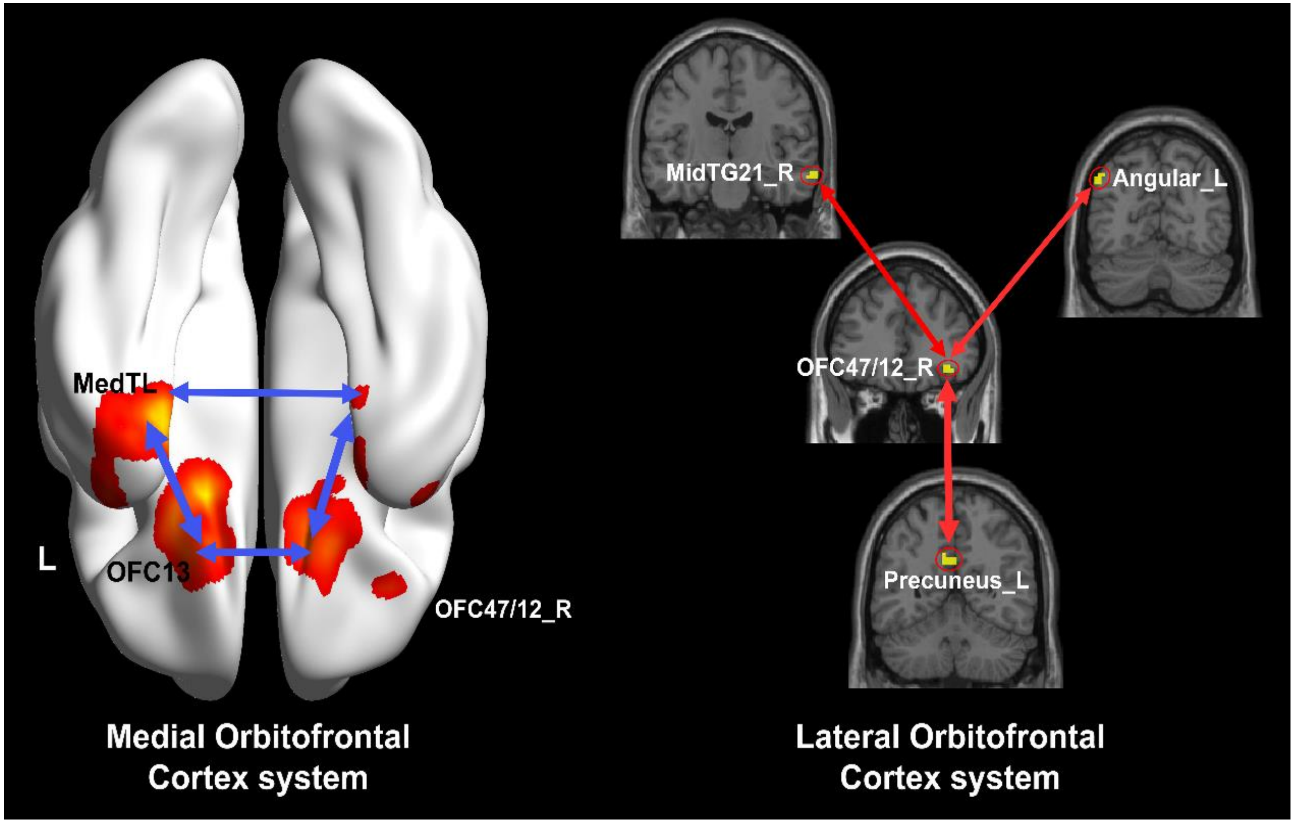
- The correlation matrix (left) and circular diagram (right) between voxels (grouped with the automated anatomical labelling atlas) shows in depression:
- Increased functional connectivity (red, yellow) between the lateral orbitofrontal cortex (related to non-reward) and the precuneus, the temporal cortex, and the angular gyrus.
- Decreased functional connectivity between the medial orbitofrontal cortex (related to reward) and the parahippocampal gyrus memory-related areas.



Cheng, Rolls et al 2016 Brain

Functional connectivity in depression

- Summary: In depression:
- Increased functional connectivity (red) between the lateral orbitofrontal cortex (related to non-reward) and the precuneus (related to the sense of self), the temporal cortex (vision), and the angular gyrus (language).
- Decreased functional connectivity between the medial orbitofrontal cortex (related to reward) and the parahippocampal gyrus memory-related areas.



Cheng, Rolls et al 2016 Brain

Functional connectivity in depression