

What can neuroscience tell us about horses?



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Neuroscience research today

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Review

The Effects of Acute Exercise on Mood, Cognition, Neurophysiology, and Neurochemical Pathways: A Review

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Abstract. A significant body of work has investigated the effects of acute exercise, defined as a single bout of physical activity, on mood and cognitive functions in humans. Several excellent recent reviews have summarized these findings; however, the neurobiological basis of these results has received less attention. In this review, we will first briefly summarize the cognitive and behavioral changes that occur with acute exercise in humans. We will then review the results from both human and animal model studies documenting the wide range of neurophysiological and neurochemical alterations that occur after a single bout of exercise. Finally, we will discuss the strengths, weaknesses, and missing elements in the current literature, as well as offer an acute exercise standardization protocol and provide possible goals for future research.

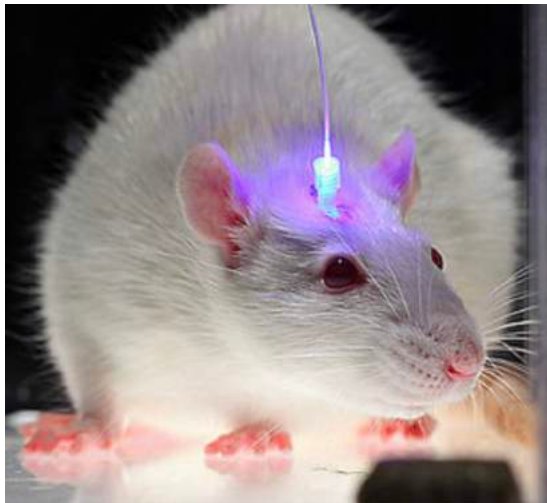
Keywords: Running, affect, prefrontal cortex, hippocampus, electroencephalography, neuroimaging, neurochemistry, neurogenesis

INTRODUCTION

The positive influence of exercise on mood and cognition across the lifespan has become a topic of much excitement [1]. In particular, abundant data suggest that physical activity can reduce the risk of various neurological diseases and protect the brain from the detrimental effects of aging [2–4]. Ani-

mal models of aging have shown that long-term exposure to exercise [7, 8]. In humans, both behavioral and functional imaging approaches have started to identify the neuroanatomical systems modulated by long-term increases in exercise. The most commonly reported area to undergo improvement is the prefrontal cortex, with exercise-induced enhancements observed in attention and other executive functions [9]. As well as for improving cognition

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<https://www.zmescience.com/medicine/genetic/draft/>

The New York Times

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Running as the Thinking Person's Sport

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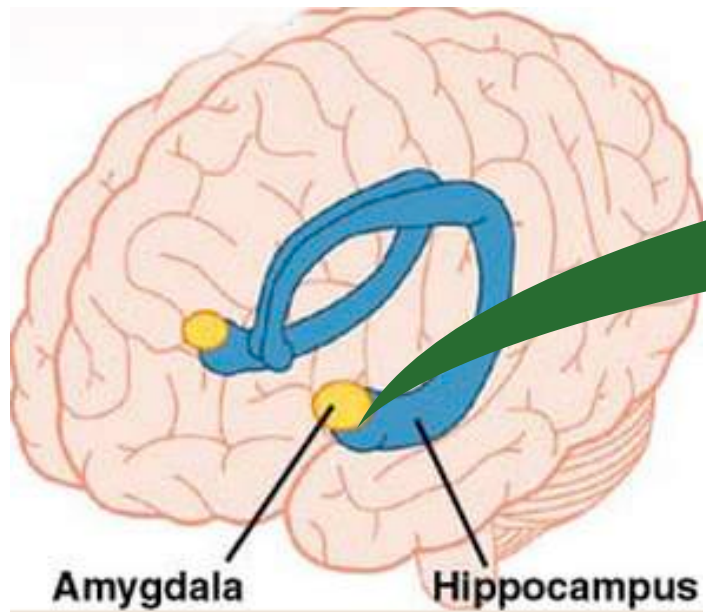
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By **Gretchen Reynolds**

Dec. 14, 2016

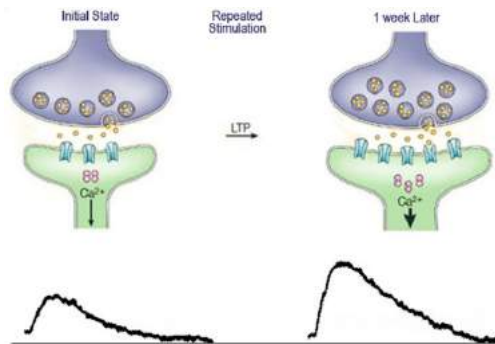
Running seems to require a greater amount of high-level thinking than most of us might imagine. The sport seems to change how the brain works in surprising ways, according to a new report.

Fear and horse training

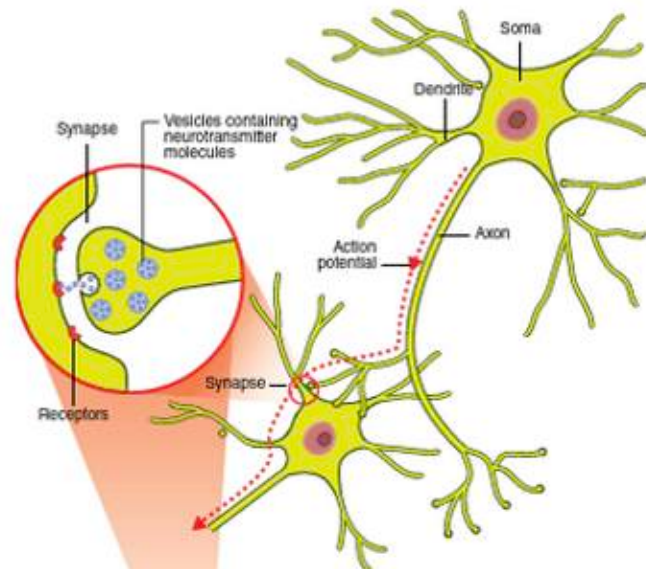


<https://horsehead.info/troubled-horses-brain/>

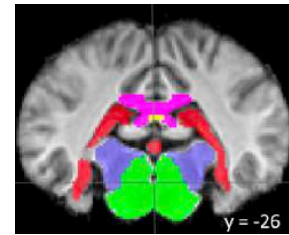
Change in synapse during learning



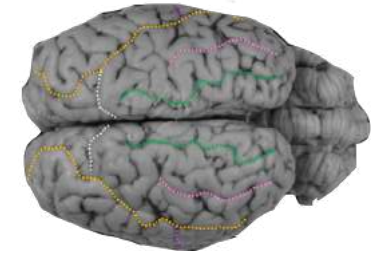
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(Reproduced from *Equine Behavior*, copyright Elsevier 2004.)



Schmidt et al., 2019, doi.org/10.1371/journal.pone.0213814



Behavioural outcome

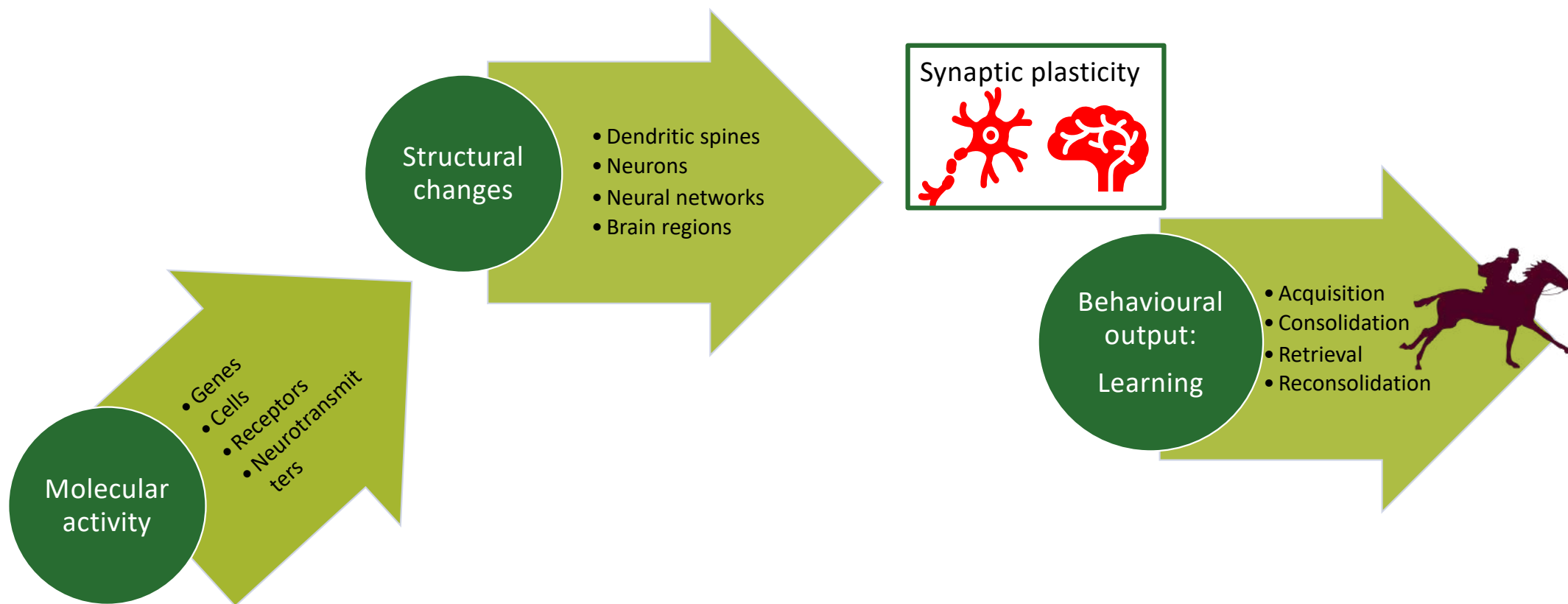
First ride



Four weeks later



From molecules to behaviour



Impacts on brain activity- influences on learning

- Stress
- Fatigue
- Fear
- Exercise
- Past experiences
- Internal state
- Genetics
- Sex of organism + many others

Learning



Associative learning

- Two forms
- Operant/instrumental conditioning
 - Goal-directed learning
 - Actions and their consequences
 - Flexible-adaptive
- Pavlovian/classical conditioning
 - Stimulus-response learning
 - Habits
 - Inflexible



Learning networks: Flexible

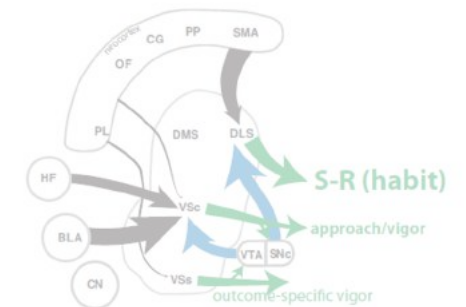
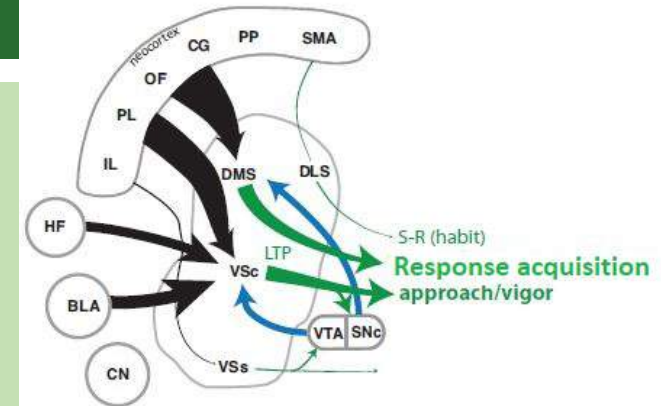
Flexible-Goal directed behaviour

- Actions and their consequences
- Instrumental learning acquisition

Flexible network adapts to environment:

- New learning
 - Reversal learning
 - Cognitive flexibility
- ## Allows for updating and flexibility when contingencies change
- ## Dopamine signalling critical for acquisition of instrumental learning
- ## Synaptic plasticity in basal ganglia, cortical areas, amygdala + others

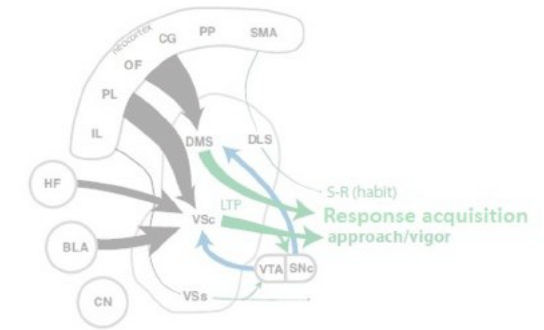
Flexible neural network



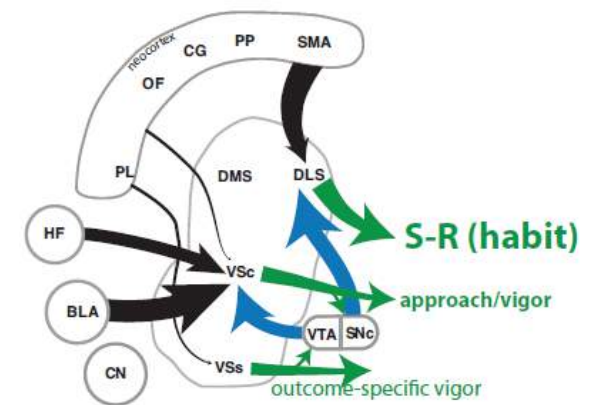
Adapted from Gruber and McDonald, (2012), Context, emotion, and the strategic pursuit of goals: interactions among multiple brain systems controlling motivated behaviour, doi: 10.3389/fnbeh.2012.00050

Learning networks-Habits

- **Stimulus-response network**
- Maintains behaviour
- Stimuli elicit responses=**stimulus-response** behaviour (e.g. responses to clicker)
- Consequences/outcomes less important for driving behaviour
- Cognitively efficient:
 - Simpler network
 - Somatosensory cortex (sensory info) to basal ganglia
 - Reduced involvement of cortical structures and eventually the amygdala
- **Brain defaults to habits** -uses less resources, frees up cognitive processing for other activities



Habit network



Adapted from Gruber and McDonald, (2012), Context, emotion, and the strategic pursuit of goals: interactions among multiple brain systems controlling motivated behaviour, doi: 10.3389/fnbeh.2012.00050

Which network is in control?

- Flexible and habit networks cooperate and compete
- Flexible network acquires new learning
- Habit network maintains it
- Habit network exerts control by inhibiting activity in flexible network
- Some forms of stress can bias habit network at expense of flexible network:
 - Adaptive: not "overthinking" decisions under stress
 - Maladaptive: impaired ability to be flexible and adapt

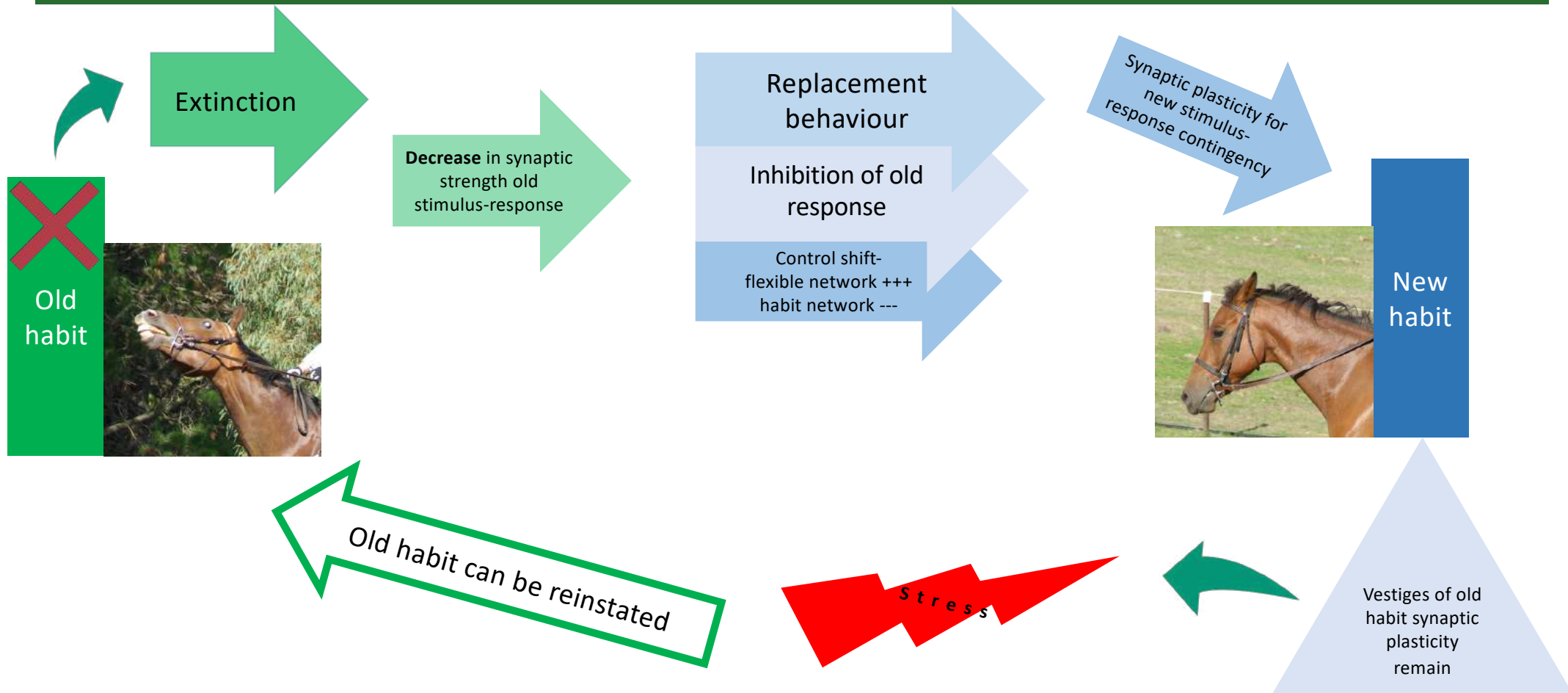


Habits in horses develop quickly and are hard to break

- Learning to quickly escape/avoid/decrease aversive stimuli is **beneficial**
- **Rapidly learned**
- Quickly shift to habits- defaulting mechanism
- Resistant to extinction
- Even after extended training in a new behaviour, vestiges of habit memories remain in neurons
- Underpins spontaneous renewal of the old habit



Cognitive flexibility-unlearning a habit



Take home for horse owners?

- Train correctly to develop good habits right from the start from the early learning controlled by the flexible system until the habit system takes control
- Practice the good habits so they are strongly consolidated in habit system
- When unwanted habits return?
 - “Disobedience”, lack of intelligence OR
 - Failure to retrieve new learning memory?
 - Failure to inhibit the old habit memory?
 - Vestiges of old habit structures in neurons?
 - Competition between flexible and habit networks?
- Reduce/avoid strong stress during retraining (including yours!) to enable flexible network to take back control and learn the new response
- Carefully practice new response so it becomes the new habit

Neural basis of decision making in instrumental learning?

■ Learning theory:

- Traditional approach to assessing animal responses to stimuli/outcomes in their environment
- Reinforcement and punishment

■ How does the horse actually experience it?

■ How does the brain process information about stimuli and responses in instrumental learning?

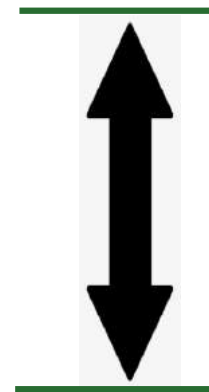
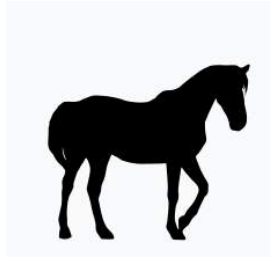


Making decisions that deliver benefits and avoid harm =instrumental learning

- Animals consistently process cues about their environments to make decisions to:
 - Maximise beneficial outcomes (gain resources/avoid adverse events)
 - Minimise adverse outcomes (lose access to resources/escape adverse events)
- New stimulus?
 - Stimulus characteristics + equine ethology + past experience influence the trial and error behaviours that result in **maximising benefit** or **minimising adversity**
- Drives the development of a **prediction** to inform future behaviour
- The “prediction error”

How does it work?

Prediction



ERROR



Reality



Next time?



The prediction *error*-the brain's "teaching signal"

The **difference** between the **predicted** outcome and the **actual** outcome



The "error"

SIZE?
VALENCE?



- Signalled by **dopamine** reward centres.
- Other neurotransmitters also involved:
 - endogenous opioids
 - endocannabinoids
 - + others

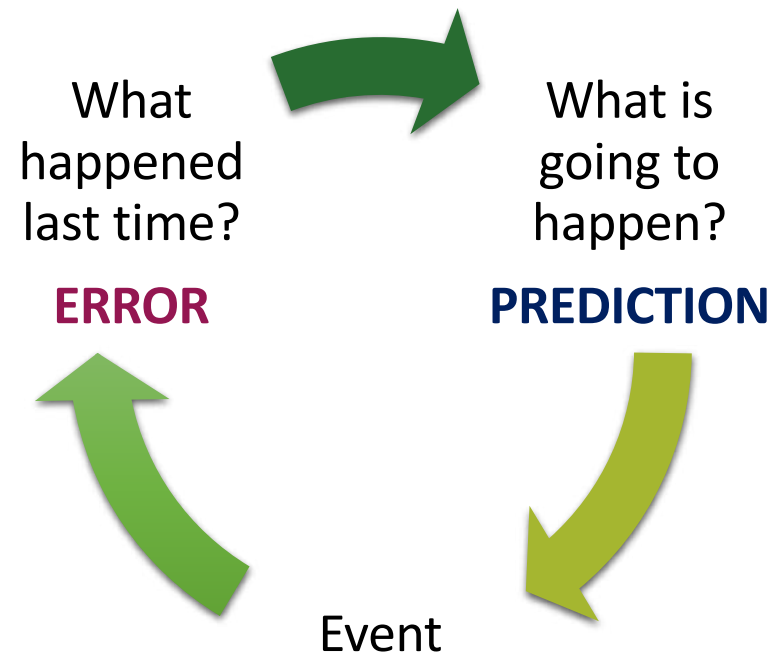


Dopamine release:

- synaptic plasticity= learning/memory
- affective influence=how it feels
- behaviour

The future and the past

- Prediction errors are **prospective** and **retrospective**
- The **error** is computed after the consequence is known
- This feeds into the **prediction** about what happens next time
- Influences the likelihood of future behaviour:
 - increase
 - maintain
 - decrease



The prediction error

- The basal ganglia and associated structures are **wired** to create these associations-facilitates adaptation in a dynamic environment:
- Predictions about cues paired with outcomes
 - “Click” from a clicker that precedes the delivery of a reward
 - Raising of whip that precedes the person hitting the animal
- Predictions about the what the response will deliver
 - Beneficial outcome (reward/avoidance of aversive stimulus)
 - Adverse outcome (aversive stimulus that must be escaped)
- Predictions about the effort required to achieve the expected outcome
- We have limited control over the formation of predictions:
 - **In our control**- loading the clicker= “click” + food = click predicts food delivery
 - **Not in our control**-sight of the white bucket prior to getting fed= bucket + food= bucket predicts food

Prediction errors can be:

Appetitive
learning
errors

Aversive
learning
errors

▪ Positive:

- Outcome is better than expected



▪ Neutral:

- Outcome is as expected



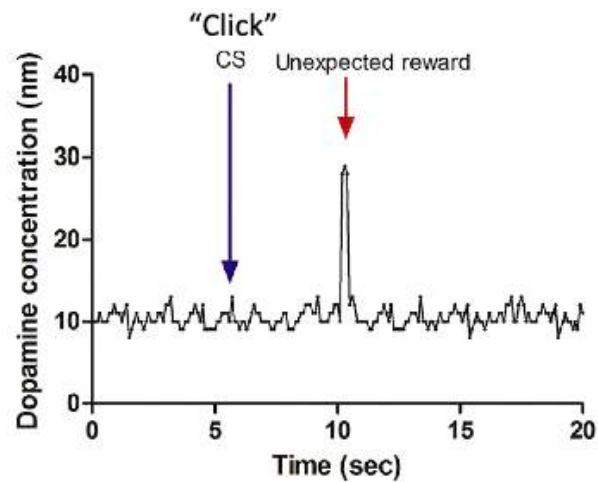
▪ Negative:

- Outcome is worse than expected

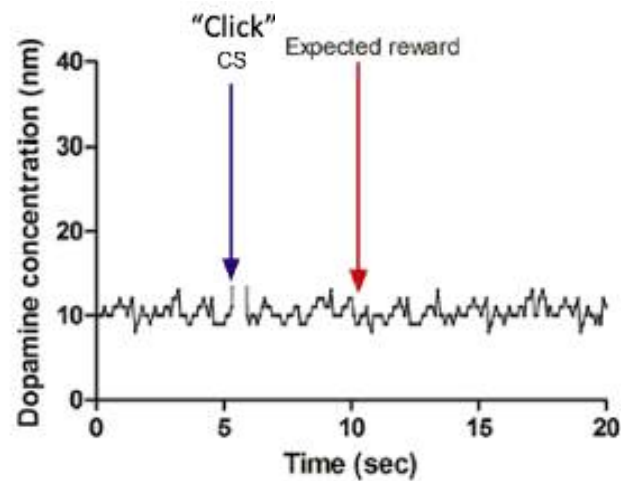


Dopamine "teaching signal"

Positive error-better than predicted

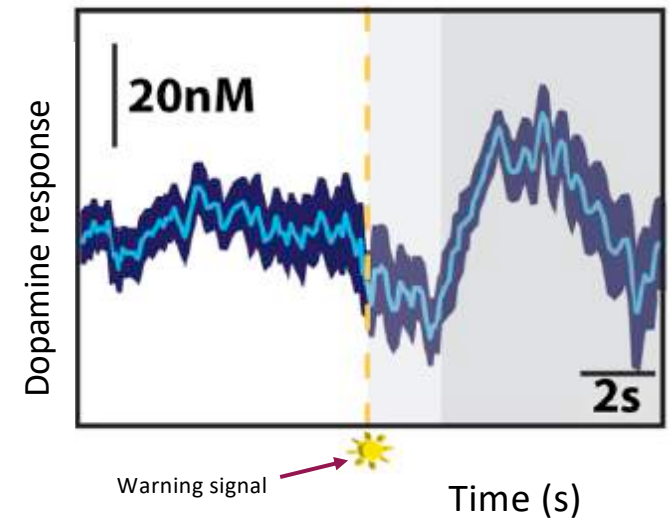


Neutral error-as predicted



Adapted from, McBride et al., 2017, Applied neurophysiology of the domestic horse

Negative error-worse than predicted



Adapted from Oleson et al., 2012, Subsecond Dopamine Release in the Nucleus Acumbens. Predicts Conditioned Punishment and Its Successful Avoidance

Factors affecting prediction errors

Valence

- Appetitive vs aversive
- Something approached (food)
- Something avoided (a whip tap)

Value

- The importance of the outcome
- How much **effort** to achieve the outcome
- The **value** of the outcome compared to other outcomes

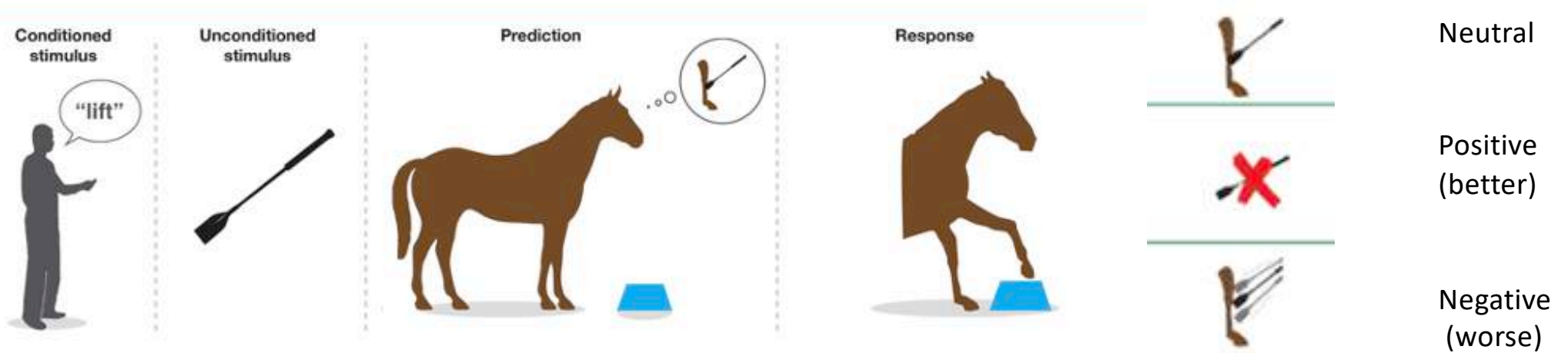
Salience

- Can the horse discriminate the stimuli from other environmental stimuli?
- Competing stimuli: Internal/external

Affective state/emotions

Making an aversive learning prediction

Possible outcomes=
Errors



Aversive learning prediction -escape

▪ Early learning or retraining type learning

- Evidence suggests the dopamine signal **does not** differentiate between punishment and reinforcement
- The aversive stimulus **decreases** dopamine activity

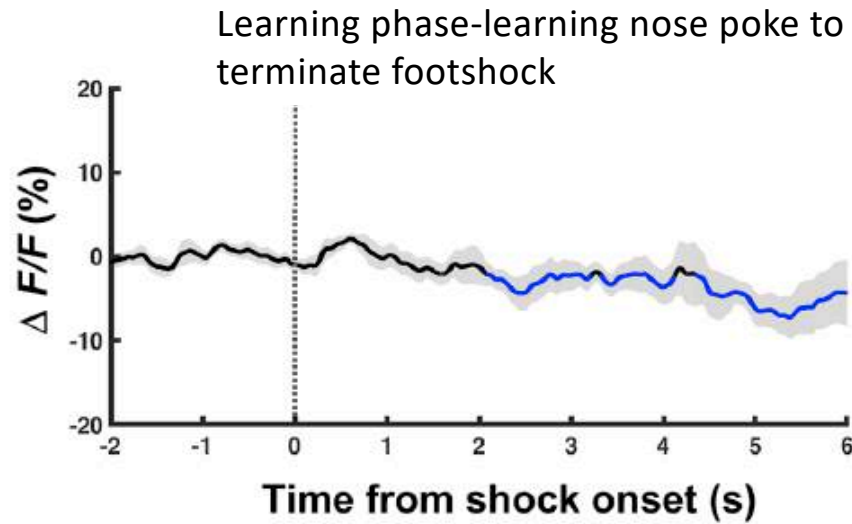
▪ HOWEVER...

▪ Later learning-rapid escape of aversive stimuli

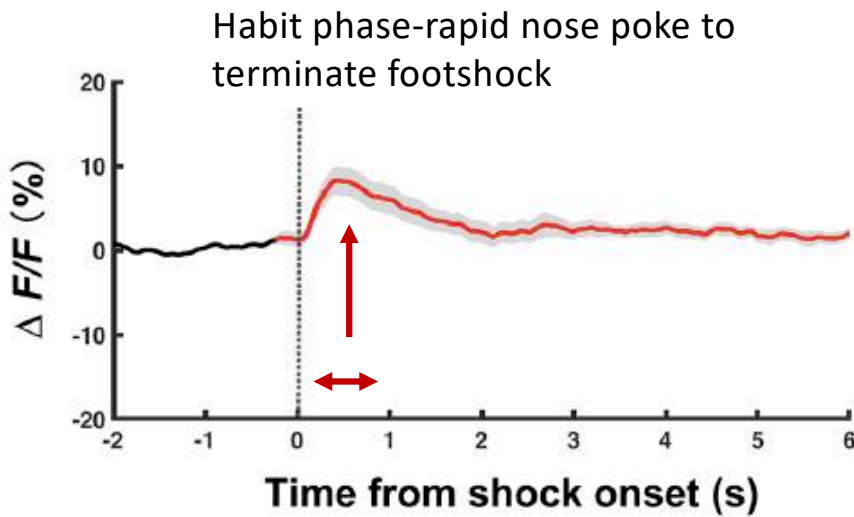
- Prediction error becomes more reliable (outcomes match expectations)
- Timing and pattern of dopamine release shifts
- Cues associated with or the aversive stimulus itself can elicit dopamine **increase**:

Note on aversive prediction errors-
Negative reinforcement

Identical presentation of inescapable footshock



Activity in dopamine releasing neurons **decreases**

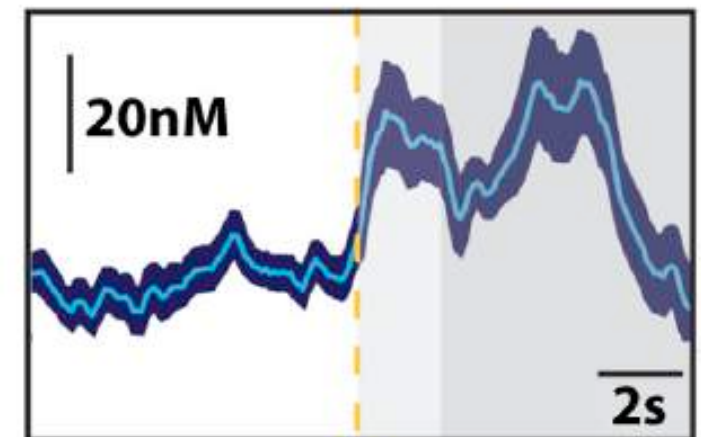


Activity in dopamine releasing neurons **increases**

Aversive learning prediction errors -avoidance

- When animals can reliably **avoid** predicted aversive stimuli they become calm:
 - ✓ Avoidance response itself becomes a predictor of **safety** from the stimulus= increase in dopamine release **BEFORE** the successful avoidance
- With extended training
 - ✓ Reduced involvement of amygdala and eventually dopamine when PE is zero
 - ✓ Behaviour is relaxed, responses repeated over long periods
- In horses?
 - ✓ Providing the opportunity to **completely avoid** or be exposed to only **very light or minor** training cues could function in similar ways.

Mean \pm SEM Dopamine Avoidance



Warning
signal

Foot shock
risk period

Safety period

Oleson et al., 2012, Subsecond Dopamine Release in the Nucleus Acumbens. Predicts Conditioned Punishment and Its Successful Avoidance

Take home message:

- Negative welfare implications of using aversive stimuli in horse training can be mitigated:
 - Facilitate the **development** of desirable habits that enable rapid **escape** from aversive stimuli during aversive operant conditioning AND
 - Reduce stimuli to the lowest levels possible as soon as possible (semi-avoidance) AND
 - Wherever possible give the horse the opportunity to **avoid** aversive stimuli through Pavlovian learning
 - This aligns with current Equitation Science advice to trainers on the use of aversive stimuli in horse training:

“Negative reinforcement should involve the use of minimal force. Aversive stimuli used to provoke a response should be used appropriately and minimally so that habituation and stress are avoided”

International Society for Equitation Science position statement on aversive stimuli in horse training, 2018

Getting predictions right



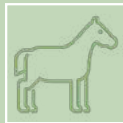
Behaviour becomes stable



Highly repeatable



Habit-resistance to extinction



Reduction in emotion

Reduced role for amygdala

Getting predictions wrong?



Can be beneficial

- Large PE? Adapt to the situation
- Change behaviour

If can't adapt-then maladaptive

- Persist with unrewarded/unreinforced or even punished behaviour
- Negative affect: dopamine suppression
- Anxiety/fear
- Defensive network activation: periaqueductal grey/amygdala?
- Flight, aggression, passivity

Predicting with a human-the horse's perspective?

- Humans can make it difficult for the horse to make accurate predictions.
- We deliver cues and consequences that are often:
 - Hard to discriminate
 - Unreliable-inaccurate PEs
 - Mismatched in value and valence (our estimation vs the horse's)
- Can the horse predict what to do to escape/avoid aversive stimuli?
- If no-large negative PE (dopamine decrease because worse than expected)
- Uncertainty-anxiety-negative emotions?
- Try other behaviours to escape/avoid
- Develop new predictions based on updated errors
- Unwanted behaviours reinforced-develop new (unwanted) habits
- Possible many training failures or unexpected responses during training result from PE issues.



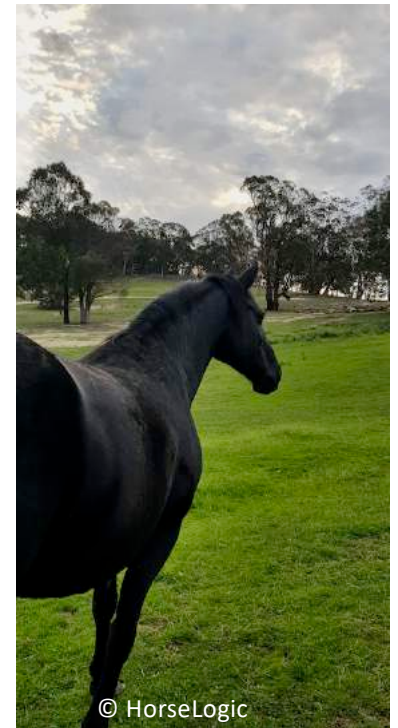
PE Take home message

- Current Equitation Science training advice provides the answers:
 - Be consistent
 - Be predictable
- Enable the horse to rapidly form **accurate** predictions about how to achieve **beneficial outcomes** for itself (achieve access to rewards or rapidly escape/avoid aversive stimuli):
 - End goal of training - PEs that are small (horse can accurately predict what's going to happen) and positive (better than it is expecting)
- PLUS-Consider the **value, valence** and **salience** of :
 - the cues,
 - the effort the horse has to put into responding,
 - and the outcome
- From the horse's perspective.



A question about aversive learning?

- Because during early learning the brain does not appear to differentiate between aversive stimuli intended to reinforce or punish behaviour...
- (Both cause a decrease in dopamine release and a cessation of the current behaviour and commencement of a new behaviour)
- Does the horse **experience** a difference between punishment and reinforcement?



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Punishment-reinforcement continuum?

- Could the horse experience punishment and reinforcement on a **continuum** as it learns to predict, escape and avoid aversive stimuli?
- The **phase of learning** could determine the shift from punishment to reinforcement in the brain's response to aversive stimuli during associative learning
- Initial acquisition of learning **versus** early and then late habit learning
- Change in valence of PE and dopamine release from **negative** to **positive**:
 - ✓ Negative PE-expectation of adverse outcome [dopamine decrease] vs
 - ✓ Positive PE-expectation of rapid escape or avoidance of adverse outcome [dopamine increase]
- Implications for how we conceptualise punishment and reinforcement and advice for horse owners?
- More research required



To conclude

- Neuroscience research can help horse owners improve their training practices to enhance horse welfare and improve rider safety
- Complements the existing body of evidence based advice already available to horse owners.
- Research in horses is increasingly incorporating neuroscience findings in the design and interpretation of results
- In addition to the areas I've highlighted today, there are many other areas that can be of benefit



Thankyou and questions?



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