Title: Question 8. How do emotion and cognition interact?

Subtitle: Can we advance our understanding of emotional behaviour by reconcepualizing it as involving valuation?

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Emotions are difficult to define, but they likely evolved from simple mechanisms that enable animals to avoid harm and seek valuable resources [1]. Simple and evolutionarily old brain systems may serve fundamental aspects of emotional processing and provide information and motivation for more recent systems that control complex behavior [2]. Here we sidestep subjective and experiential phenomena of emotion and focus on the observation that emotions have quantifiable and distinct objective consequences in the behaviours they evoke – for example, facial, postural and approach behaviours differ unmistakenly between anger and desire. Because only one or a few behaviours amongst the many potential ones can be expressed at any one time, emotional guidance of behaviour effectively implies a choice between multiple different options, and hence a relative valuation of these options.

Taking the view of valuation allows us to recast the classic distinction between emotions and cognition [3]. We ground this approach in a long history of associative learning theory. This addresses how animals learn and represent the value of actions and states in the world and has strongly argued for the existence of multiple separate valuation systems [4][5][6]. We highlight in particular a dichotomy between an evolutionarily older Pavlovian and a more recent instrumental valuation system. In Pavlovian scenarios, values are attached to stimuli independently of actions, while in instrumental scenarios values are attached to actions in a manner that is tied to the presence of particular stimuli [7][8][9][10]. Importantly, only instrumental values can implement any kind of behavior, while Pavlovian values depend on innate mappings between the stimulus and actions, e.g. approach and food. Pavlovian values are effectively restricted to modulating innate – henceforth 'Pavlovian' – responses.

The specific aim of this essay is two-fold. First, we describe how effects of emotion on cognition and behavior can be conceptualized as reflecting an impact of innately specified Pavlovian responses to valued stimuli on learning and decision-making. Second, we exemplify the exquisite vulnerability of Pavlovian-instrumental interactions to changes in the major ascending neuromodulatory systems, rendering them core features of several neuropsychiatric disorders characterized by abnormal emotional processing [11,12].

Pavlovian responses

The power of the Pavlovian innate responses is well illustrated by a classical experiment by Hershberger [13] here chicks were placed in front of a food cart. The food cart was set up to move in the same direction as the chick but at twice the speed. Thus, to obtain the food, the chick had to move away from the food cart so the cart would speed towards it. The chicks were unable to overcome the (usually adaptive) innately specified tendency to approach the positively valued food. By analogy, raccoons continue to 'wash' food-related objects even when they actually need to release these objects to obtain the food [14]. Similar species-specific behaviours can also be observed in porpoises, cats, dogs, hamsters, pigs, cows and even whales.

The influence of Pavlovian response tendencies on behaviour has probably best been experimentally isolated in Pavlovian-to-instrumental transfer (PIT) paradigms. Here, subjects are asked to perform instrumental tasks (e.g. pressing a lever for food) and separately undergo classical conditioning. The PIT effect consists in these task-irrelevant Pavlovian stimuli modulating the instrumental responses (in extinction), with positively and negatively valued stimuli, respectively, increasing and decreasing responding for reward [15][16][17].

Similar Pavlovian effects are seen in humans, both in appetitive [18,19] and aversive [20] domains, and recent studies have highlighted the existence of PIT in humans [21][22][23]. Stimuli with putatively innate value (e.g. happy and angry faces [24]) also influence behaviour in humans much in the same way as the food was attractive to the chicks. In approach-avoidance paradigms, people respond more slowly when approaching angry faces than when avoiding angry faces (and vice versa for happy faces). Critically, the degree of slowing is predicted by the degree to which the angry (versus happy) face elicits bodily freezing [25]. Bodily freezing is one of the most widely

recognized defensive reactions to threat [26]. It can be reliably measured in humans using posturography and is associated with bradycardia. Accordingly, the finding that the interference with approach due to putatively innately valued images can be predicted by the degree of bodily freezing strongly suggests that Pavlovian biasing of action involves the influence of a system that also controls innately specified responses.

Emotions and valuation

Both Pavlovian and instrumental values can be derived through model-free or model-based valuation mechanisms. Model-based valuation depends on an understanding of the structure of the world. Stimuli acquire value by inferring the implied future consequences within this model. This requires processing power, but is flexible. Model-free valuation by contrast, is retrospective and assigns value to states or stimuli according to their past consequences. At the time of choice, model-free values are computationally cheap, but they demand substantial experience to be accurate. Hence, these two systems trade experiential for computational costs – one changes slowly with experience, the other rapidly but requires substantial cognitive resources. Together, this formulation leads to a quartet of values: model-based and model-free Pavlovian values, and goal-directed (model-based) and habitual (model-free) instrumental values [27].

Broadly speaking, model-free and model-based Pavlovian valuation might map onto automatic and cognitive accounts of emotions. In the automatic view, stimuli activate emotional centres, which dictate responses largely foregoing any contact with cognition. In polar opposition, cognitive theories suggest that human emotions predominantly *follow* cognitive assessments [28]. The argument here is that emotional responses concern the recruitment of innate response patterns (approach, fight, flight etc.) to particular valued stimuli, but that this valuation can arise both through model-based or model-free Pavlovian valuation [8][29][27], with the former mapping more closely onto cognitive and the latter onto automatic views of emotion.

Clearly, these valuations coexist and can compete for expression, forming one path for how 'emotion' and 'cognition' may interact. However, Pavlovian responses can also directly influence the mechanisms of model-based instrumental valuation. Specifically, we have shown that Pavlovian inhibitory suppression influences cognitive planning [30,31]. In a planning task that was too complex to fully solve, subjects were forced to make a variety of approximations in their internal evaluation of action plans. When examining the pattern of choices, we observed that subjects were substantially impaired when the optimal action sequence involved a salient loss. Depending on the size of the salient loss, this could be adaptive and reduce computational cost without affecting performance, but it was essentially unchanged and persisted even when it led to very substantial overall losses. This led us to conclude that it may be the signature of an inflexible, reflexive response to the internal occurrence of a loss event, and to argue that it was akin to an internal Pavlovian response. Therefore, we conclude that Pavlovian behavioural inhibition can shape highly flexible, goal-directed choices not just by competing with the resulting actions, but by influencing their internal evaluation.

Role of serotonin

Pavlovian-instrumental interactions are exquisitely sensitive to changes in the major ascending neuromodulatory systems. The neuromodulator that is perhaps best known to impact both emotion and action is serotonin. In particular, it is implicated in both aversive emotional processing [32][33] and behavioral inhibition [34], with evidence showing that a reduction in serotonin disinhibits behavior in the face of expected punishments [35][20][36]. This work provided the basis for ideas that serotonin has a specific role in tying aversive Pavlovian influences to instrumental inhibition [11][37]. For example, Dayan and Huys [38] have argued that serotonin deficiency, as seen in depression, leads to a failure to inhibit aversive thoughts and actions. We provided empirical evidence supporting these hypothesized effects of serotonin in mediating the effects of the Pavlovian on the instrumental system in humans using acute tryptophan depletion to deplete central serotonin levels (ATD [39]). Geurts et al [23] found that under normal levels of serotonin, aversively conditioned stimuli inhibited instrumental responding, yet when serotonin levels were depleted, this response inhibition was released.

These PIT findings support the notion that serotonin modulates aversive Pavlovian-to-instrumental transfer. However, there are also discrepant findings. Notably, there are a number of studies that report motivationally driven but valence-independent effects of both appetitive and aversive cues on action of altered serotonin levels [40][41]. In addition, even seemingly opposite effects of punishment-predictive cues, i.e. increased aversive PIT after tryptophan depletion have been reported [42]. Finally, there are several studies suggesting a potential role of serotonin in appetitive processing [43–45][46]. Accordingly, the precise role of serotonin in valuation and Pavlovian responses remains to be determined.

Pavlovian responses gone awry

Aberrant interactions between Pavlovian and instrumental control systems might well play an important role in the emotional decision-making anomalies seen in neuropsychiatric disorders. One exemplary neuropsychiatric consequence of deficient Pavlovian-instrumental interaction is psychopathy. Psychopathy is characterized by several affective and emotional anomalies, such as lack of remorse, guilt and empathy [47]. A core feature is instrumental aggression [48], a form of aggression that is premeditated and used at the expense of others to achieve a desired goal (e.g., to obtain a victim's money). Psychopaths are typically not affected by emotional cues (e.g., facial expression of a suffering victim) that would normally discourage instrumentally aggressive acts [49]. In keeping with these characteristics, we found that the instrumental choices of violent offenders with psychopathic traits were unaffected by angry emotional faces. Specifically, violent offenders showed reduced instrumental avoidance in the context of aversive (versus appetitive) faces relative to non-criminal controls (Ly, Von Borries, Brazil, Bulten, Cools and Roelofs, submitted). Thus, psychopathic tendencies were accompanied by deficient transfer of Pavlovian value to systems that control instrumental action. Moreover, in a separate study we found that increased psychopathic severity was associated with reduced aversive PIT (Geurts, von Borries, Huys, Bulten, Verkes and Cools, in preparation). Taken together, these results suggest that, rather than studying aversive processing per se, an understanding of the behavioral anomalies of psychopathy requires us to study the *consequences* of aversive processing for instrumental action, a process that is largely unexplored in this population.

The finding that criminal psychopathy is accompanied by reduced aversive Pavlovian-instrumental transfer is remarkably consistent with the reduction in aversive PIT after central serotonin depletion [23]. Serotonin metabolites, and hence probably serotonergic transmission, is known to be reduced in criminal psychopathy (indexed by the PCL-R Score, [50]), and we have found a strong correlation between the PCL-R score and aversive PIT. This suggests that aversive Pavlovian disinhibition in psychopathy might be countered by serotoninergic medication akin to the reduction in provoked aggression seen in primary psychopathy with paroxetine, a selective serotonin reuptake inhibitor [51].

Conclusion

We have redefined and narrowed down the question of 'how do emotion and cognition interact' by focusing on how innately specified Pavlovian responses to valued stimuli can influence learning and decision-making. We believe that this approach allows us to bring a wealth of knowledge about behaviour and decision-making and their neurobiological mechanisms to bear on accounts and disorders of emotional processing. Of course, this approach also raises very important questions about the conception of emotions: are emotions immediate subjective correlates of valuation, or do they arise indirectly through the perception of the associated Pavlovian responses?

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