

Rethinking Core Affect: The Role of Dominance in Animal Behaviour and Welfare Research
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[draft]

Abstract

The study of affective states increasingly demands the integration of philosophical and experimental research. This paper contributes to this interdisciplinary endeavour by examining theoretical assumptions underlying the experimental study animal affective states. Within this context, functional operationalization stands as a powerful tool in guiding researchers' quest to construct cross-species measures and tractable hypotheses concerning the stimuli that trigger these states and the ensuing responses they elicit. However, standard reliance on valence-arousal models, where positive valence aligns with rewards and negative valence with punishments, imposes questionable constraints on such task. In settings that are closer to ecologically relevant situations, animals routinely encounter a diverse array of stimuli, some of which elude neat categorization as purely rewarding or punishing. This complexity prompts a compelling case for the (re-)integration of *dominance* as a dimension of affect –a conative dimension that offers a more nuanced framework for explicating the affective responses of animals. To do so, this paper engages with the theoretical and methodological challenges surrounding the incorporation of a third dimension in the definition of core affect, advocates for a definition of dominance as a measure of self-assessed behavioural control and, on such basis, proposes the 'Valence-Arousal-Dominance' model of affect. Finally, the paper explores the model's prospective applications on the study of animal affect-related decision-making under predation risk and its potential to unlock new methods for improving animal welfare.

Keywords: emotion – animal personality – boldness – judgment bias – decision-making – core affect

1 Introduction

Animal affectivity constitutes a thriving area of research within the field of non-human animal (henceforth “animal”) behaviour and biology (Mendl & Paul, 2020; Neethirajan et al., 2021). There is an increasing recognition that affective phenomena, encompassing emotions, moods, and personality (also referred to as “temperament”), exerts a pivotal influence on animal’s decision-making and welfare (Mellor, 2016; Webber et al., 2022). Despite some arguments questioning the explanatory value of animal’s affect (e.g., LeDoux, 2022), growing interest on the ecological consequences of individual’s differences in behaviour, including affect-related decision-making, underscores the significance of investigating this aspect of animals’ life (Bračić et al., 2022; Laskowski et al., 2022). To investigate affective states, philosophers and psychologists have proposed different models delineating what emotions amount to (Moors, 2022; Schiller et al., 2022). While “discrete” models focus on the characteristics of distinctive emotion categories such as anger or joy, “dimensional” models break down these categories into primitive components such as “valence” and “arousal”, presumed to regulate physiological activities across species (see Kremer et al., 2020).¹

This paper evaluates some of the limitations encountered when applying the “Circumplex” (valence-arousal) model of affect to the domain of animal behaviour and welfare science, in particular through the Judgment Bias Test (JBT) paradigm. The JBT explores the influence of affective states on behavioural decision-making by measuring animals’ relative level of bias to perceive ambiguous stimuli as expecting rewarding (i.e., “optimism”) or punishing (i.e., “pessimism”) (Harding et al., 2004; Paul et al., 2005). While relying on valence-arousal models of affect (e.g., Mendl et al. 2010), the JBT has been applied to a variety of species, spanning mammals and fish, thus demonstrating that its main predictions are supported (Lagisz et al., 2020). However, psychologist have observed that the Circumplex model faces limitations in effectively capturing qualitative variations in individual’s attitudes towards risk, whether occurrent (e.g., fear), or dispositional (e.g., boldness) (e.g., Carver & Harmon-Jones, 2009). This, in turn, restricts research on animal affect, given that foraging decision-making requires animals not only to anticipate positive or negative outcomes but also to evaluate the trade-offs between feeding and safety. Therefore, to capture emotions’ influence on how animals navigate their environment or *Umwelt* (Uexküll, 1934), we require a more nuanced framework.

To address this limitation, I propose an alternative model that (re-)incorporates a third affective dimension, namely “dominance”. Dominance was featured in the early “Pleasure-Arousal-Dominance” (PAD) model, where it was defined as the subjective sensation of influence or control experienced by individuals within their environment (Mehrabian & Russel, 1974). However, it was soon considered peripheral to “core affect” (i.e., valence [pleasure] and arousal) due, among other reasons, to its “cognitive” character (Russell & Barrett, 1999). After addressing these criticisms and reevaluating the epistemological status of dimensional models of affect, I define dominance as the **subjective experience of behavioural (self-)control vis-à-vis environmental challenges** (Section 3) and elucidate how its incorporation can pave the way to a more comprehensive understanding of animals’ attitudes towards risk in ecologically relevant scenarios (Section 4). Lastly, I briefly discuss how dominance can also shed light on the study of animal welfare, and thus may not only facilitate the study of how emotions influence animals’ survival but also their thriving.

¹ In the ensuing discussion, I assume that emotions, such as anger or joy, are feelings directed towards objects or events, as supplied by their cognitive bases (e.g., perception) and that moods, such as grumpiness or elation, are long-term, occurrent states that lack an object and are caused by emotions of the same affective colour (and vice-versa). Feeling fearful, for instance, may cause someone to be in a grumpy mood, and being grumpy may cause someone to feel fearful (see Deonna & Teroni, 2012). Lastly, I assume that personalities such as being aggressive or friendly, specially within the context of behavioural ecology, are stable dispositions to experience emotions or moods contingent upon contextual cues (Kaiser & Müller, 2021; see also Réale et al., 2007).

2 Background

2.1 Dimensional models of affect

Empirical research on emotions standardly relies either on discrete or dimensional models. Discrete models conceptualize emotions, such as anger or fear, as natural kinds with specific behavioural, physiological, and neural fingerprints (Ekman, 1984; Panksepp, 1998). For instance, Panksepp's (1998) research on "genetically ingrained brain emotional operating systems", which he marks with capitalized terms such as RAGE or PLAY, has revealed various similarities in their underlying neuronal bases across mammals. However, the search for emotions' distinctive patterns has yielded mixed results. Critics point out, for example, that different outcomes (e.g., different patterns of autonomic activation) can be associated with a single emotion-type and, conversely, different emotion-types (e.g., anger and joy) can be associated with similar physiological responses (Barrett, 2017), thus raising doubts about whether current techniques are able to detect these fingerprints.

Alternatively, dimensional models view affective phenomena as composed of fundamental building blocks such as, e.g., "arousal" (i.e., degree of excitement), considered to regulate various types of primary functions across species, such as feeding or mating. Different dimensional models have been proposed, including (but not limited to) the Circumplex model (Russell, 1980), the Vector model (Bradley et al., 1992), and the Positive activation - negative activation model (Watson & Tellegen, 1985). A notable advantage of this perspective is that it allows unifying diverse types of affective phenomena within a multi-level framework. Indeed, these models not only aid in generating measurements for short-term affective states like emotions (e.g., anger) but also long-term states such as moods (e.g., elation) and personality traits (e.g., boldness). This helps drawing clearer hypotheses about an individual's affective experiences across different timeframes (Mendl et al., 2010).

Importantly, in the context of research on animal affect, dimensionality also enables the generation of measurements for the candidate behavioural, neuronal, or cognitive manifestations of affective experiences without assuming that organisms consciously witness these (Rolls, 2005). Indeed, while it is standardly considered that basic emotions such as anger or joy are consciously experienced, affective dimensions like arousal may, but don't require to, be the object of conscious awareness (Barrett, 2017). Therefore, dimensional models allow the study of affective states across species, including those whose phylogenetic distance to vertebrates (especially mammals) makes it uncertain whether they have developed awareness of their own bodily sensations (Lagisz et al., 2020).

2.2 Circumplexity and its limitations

Among dimensional models, the Circumplex model holds a prominent position in both human and animal research (see Zachar & Ellis, 2012). Proposed by Russell (1980), this model employs dimensions such as valence (positive or negative) and arousal (low or high) to characterize and measure emotional experiences. Valence corresponds to the hedonic quality of the internal state, that is, whether a stimulus is experienced as pleasurable or not. Arousal, in turn, corresponds to the level of physiological activation or energy involved in the experience. As figure 1 illustrates, delight can be characterized as a positive, high-arousal state, whereas boredom can be denoted as a negative, low-arousal state.

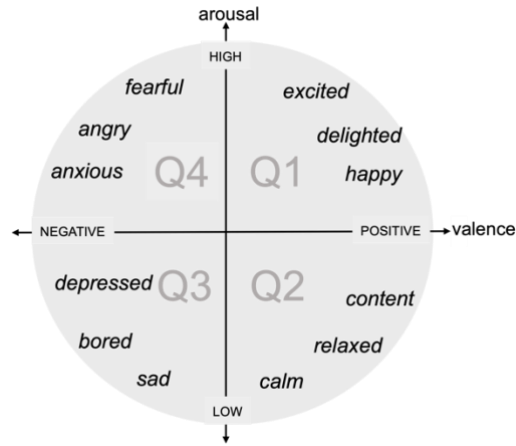


Fig. 1 Circumplex Model of Affect adapted from Russell (1980), with the X-axis representing the valence dimension and the Y-axis the arousal dimension. Words in italics indicate the location of specific affective states, including emotions

However, in human psychological research, this model has encountered criticism due to its limitations in effectively differentiating between qualitatively different negative emotions (Scherer, 2005; Carver & Harmon-Jones, 2009). For instance, even though states like anger and fear may be located in a similar region of the two-dimensional space (negatively valenced high arousal, see figure 1), they have different, and even opposite, impacts on cognitive and behavioural processes. Indeed, there is evidence that, whereas anger reduces the perception of risk, fear amplifies it (Lerner & Kelner, 2001).

Animal behaviour research relying on this model often carries such limitations. In Mendl et al (2004), for instance, the activation of positive states is linked with a “reward acquisition” system (RAS) and that of negative states with a “punishment-avoidance” system (PAS). These are biobehavioural mechanisms that guide the organism in obtaining fitness-enhancing rewards (e.g., food, shelter, etc.) or avoiding exposure to fitness-threatening punishers (e.g., predator attack, thermal damage, etc.), respectively (Watson et al., 1999). The resulting functional perspective on the structure of core affect is depicted in figure 2:

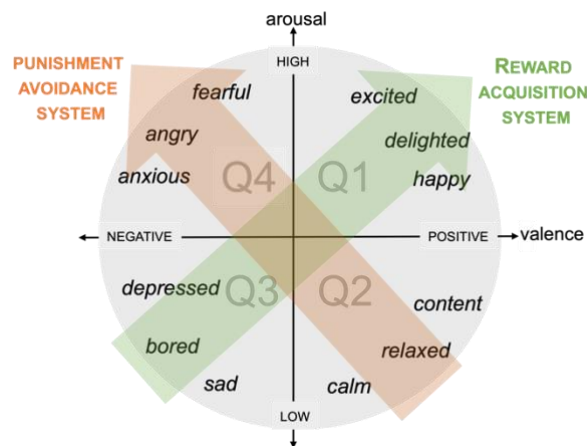


Fig. 2 Functional operationalization of the Circumplex Model, adapted from Mendl et al. (2010). Arrows indicate the link between the reward acquisition system and the Q3-Q1 axis (green), and the punishment avoidance system and the Q2-Q1 axis (red)

However, in ecologically relevant contexts, animals also encounter stimuli that possess rewarding and punishing features simultaneously (Bračić et al., under review). For example, whereas substantial rewards may entail risk when accessed, smaller rewards may be easily attainable. Thus, in the context of foraging under predation risk, the act of approaching or avoiding a stimulus don't straightforwardly map to positive or negative responses, but rather to different attitudes towards food and safety trade-offs. Some organisms may assign a higher value to potential feeding opportunities than safety and, conversely, others may assign a higher value to their integrity than the prospect of food, contingent not only on past experiences or their current energy level, but also their attitudes. Therefore, despite their many advantages in generating tractable hypotheses about animals' expectations, current valence-arousal models are not suited to expand our understanding of individuals' affective-related decision-making during foraging under predation, which is pivotal within ecological and evolutionary processes.

2.3 Some theoretical amendments

In this section, I briefly contrast three strategies to enhance dimensional models within the study of human affect. To distinguish qualitatively different states, constructivist theories incorporate a categorization process between the experience of affect and its outcomes, as roughly represented by the blue arrows in figure 3 (Barrett, 2017). Within this perspective, emotions emerge from individuals' conceptualizations of their sensations of valence and arousal. Accordingly, labels such as "anger" and "fear" denote different concepts that individuals apply to their heightened negative sensations based on contextual factors. Yet, while it is standardly agreed that affective states possess cognitive underpinnings (Deonna & Teroni, 2012), it is unclear whether, and how, animals would acquire the conceptual knowledge believed to underlie their emotional experiences (Scherer, 2009).

Alternatively, appraisal theories incorporate a stimulus evaluation process between what is perceived and the experience of affect, as depicted by the green arrow in figure 3 (Ellsworth & Scherer, 2003). To the extent that appraisals play a crucial role in characterizing emotions, these theories are thus compatible with a dimensional view of affect. Thus, the qualitative difference between overlapping states in the valence-arousal space would result from the type of appraisal giving rise to each. For instance, fear and anger would be caused by the assessment of the triggering stimulus as dangerous or offensive, respectively. However, this view raises concerns regarding the causal relationship between appraisal and affect (Moors, 2013). If appraisal causes a valenced state, which is itself often conceptualized as a form of appraisal, then it becomes unclear why one would precede the other.

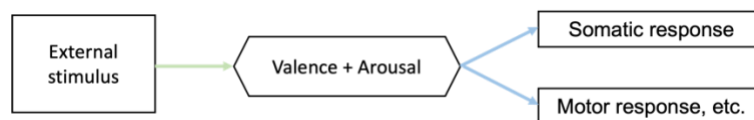


Fig. 3 Sketch of appraisal and constructivist strategies. The green arrow stands for the appraisal process, which is stipulated to trigger bodily sensations, and the blue arrows for the construction process, by which such bodily sensations are categorized

A third option is to ascribe to a yet-to-be-determined type (or types) of appraisal the same status as the other two affective dimensions, i.e., to conceive it as part of core affect itself (Fontaine et al., 2007). In this view, instead of assuming that valence and arousal offer a predefined, optimal approach to characterize the whole spectrum of affective states, affect is deconstructed into dimensions tailored to the researcher's aims insofar as their relevance to the research question at hand, grounds of their plausibility, and ability to generate tractable hypotheses, can be firmly established (Moors, 2022, p. 260). In what follows, I argue that, to investigate animal's affect-related decision-making in ecologically relevant contexts, dominance is one such candidate.

3. The Dominance dimension

3.1 Initial prominence and decline

The concept of dominance was introduced in the ‘Please-Arousal-Dominance’ (PAD) model of affect proposed by Mehrabian & Russel (1974). This model was initially applied within the “Semantic Differential Technique” framework, which aimed at measuring the affective meaning of emotion-related words and other stimuli, such as facial expressions, using bi-polar scales (Osgood, 1952). In these studies, participants were asked to rate the degree to which they perceived a stimulus as pleasant (positive-negative), arousing (high-low) and dominant (dominant-submissive). Later, the PAD model extended its scope of application, encompassing the development of metrics for emotions (Russel & Mehrabian, 1977) and personalities (Mehrabian, 1996). Illustrated in figure 4, Mehrabian (1996)’s model locates “Hostile” and “Anxious” personalities within the (-P, +A) region, but associates a higher degree of dominance with the former, thus accounting for their divergent outcomes.

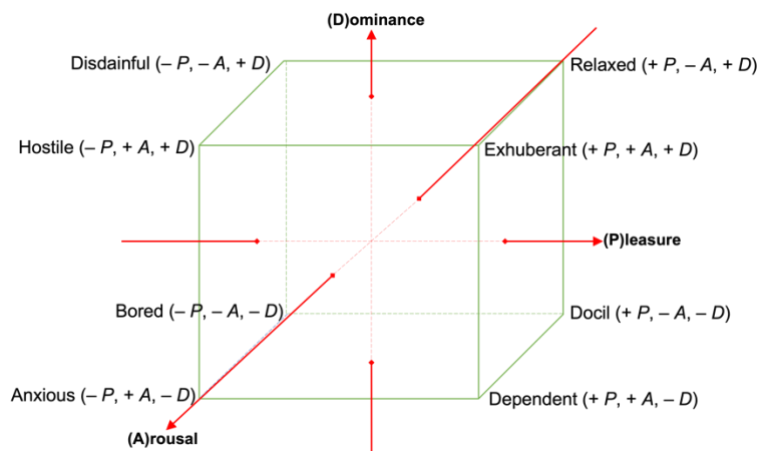


Fig. 4 PAD model’s space of personality traits adapted from Mehrabian (1996)

In this framework, dominance was initially described through expressions such as “controlling”, “influential” or “autonomous” (Mehrabian & Russel, 1974). Subsequently, it was described as denoting individuals’ feeling of control over events or their immediate surroundings (Russel & Mehrabian, 1977). This latter definition emphasizes that, while dominance may correlate with observable qualities, such as individual’s capacity to exert influence, it remains a subjective phenomenon. However, it was soon found that participants in the semantic differential technique studies often struggled to rate stimuli along the dominance dimension and that their stimuli ratings along dominance were not always independent of the other two dimensions, especially pleasure (Russell & Mehrabian, 1977). As a result, Russell (1978) redefined dominance as denoting assessments of the antecedents and consequences of the affective experience, thereby acknowledging it as a cognitive process, peripheral to the experience of affect (p. 1166).

The exclusion of dominance as an affective dimension had an enduring influence in subsequent theorizing about emotions. As observed in Section 2.3, The PA dimensions of the PAD model grounded the development of the Circumplex model of affect (where pleasure is referred to as “valence”). Then, within the constructivist framework, core affect is exclusively composed by valence and arousal, "by definition, but the definition was chosen on the basis of a long history of empirical research" (Russell & Barrett, 1998, p. 812). In sum, the exclusion of the dominance dimension arised from inconsistent statistical results within the semantic differential technique framework and its ambiguous status as either an intrinsic or peripheral component of core affect.

3.2 Addressing conceptual issues

An important source of concern revolves around the unclarity of the dominance concept (Bakker et al., 2014). Dominance has often been described using predicates that have an evaluative character (e.g., “powerful”), which may explain why it failed to arise as independent from the pleasure (valence) dimension. Moreover, the technical use of dominance in this framework may evoke the picture of dominance relations within social hierarchies². That is, with comparative, rather than individual, traits of social organisms. Therefore, since verbal reports within the semantic differential technique framework are typically about stimuli in isolation (e.g., words), we may understand why participants struggled to rate them along an (affective) dominance scale.³

Moreover, the rationale behind the location of dominance as a cognitive component bears some shortcomings, as researchers nowadays acknowledge that the demarcation between cognitive and non-cognitive processes is not as clear-cut as standardly considered. Emotions, for example, not only have cognitive bases (e.g., are anchored on individual’s perception or memory) but also possess representational properties, i.e., qualify stimuli as being a certain way and may be subject to rational justification (see De Sousa, 2003). Within evolutionary psychology, it is standardly considered that emotions evolved across species to coordinate adaptive responses through behavioural control (e.g., Frijda, 1994). If so, it becomes surprising that dominance, which precisely highlights individual’s internal state of behavioural control or influence over their surroundings, is considered peripheral to affect.

Finally, it is worth noting that, even though models of affect can be subordinate to specific theories, they can also be conceived as relatively independent from them (for an overview of different degrees of independence, see Frigg & Hartmann, 2020), particularly on cases where, by so doing, researchers can generate tractable hypotheses about emotions’ effects. Within animal behaviour and welfare research, for example, discrete or dimensional models of affect can serve as abstractions that allow defining input conditions (e.g., scenarios that precipitate a particular affective state), generate measurements of emotion’s different effects on organisms (e.g., determine types of decision-making in those scenarios), and thereby probe causal dependencies between them. Within that inquiry, theories that define core affect as solely composed of valence and arousal, often based on human reports, establish restrictions on the types of hypotheses that can be formulated.

In sum, the assumption that human introspection and verbal reports grant a privileged access to core dimensions of affect is unwarranted, as it often relies on isolated stimuli. Moreover, the criteria to delimitate between what is inherent and peripheral to affect is problematic, and models of affect within different scientific endeavours don’t need to be subordinate to full-fledged theories of affect. However, as mentioned above, putting dominance on a better ground requires to redefine it as an individual trait. As we will see next, this can be done by highlighting one of its features, namely, “(self-)control”.

3.3 Redefining Dominance as (self-)control

² Even though affective dominance could conceivably relate to animals’ social hierarchies, in this paper I will only focus on the influence of dominance in animal’s foraging decision-making.

³ Recent studies show that individuals do indeed factor on the dominance dimension when assessing facial expressions, considered among the most important means of expressions of human affect (Oosterhof & Todorov, 2008). Note that facial morphology encapsulates not only affective but also social information, which is likely to provide the necessary dynamism to make dominance arise as a relevant criterion of assessment.

The psychological literature on (self-)control offers a more robust foundation for defining dominance. To begin with, Gregory (1978) proposed that individuals evaluate control separately of whether the events are appraised as positive or negative. According to him, the regulation of positive events entails attaining a positive reinforcer, while the regulation of negative events involves avoiding aversive circumstances. Later on, Rothbaum, Wisz, and Snyder (1982), argued that individuals can evaluate their control in response to events in two different ways: “primary control”, which pertains to attempts to align events with one’s desires, and “secondary control”, which involves attempts to adapt oneself to environmental influences.

Based on these insights, Bryant (1990) examined the interplay between primary/secondary control and positive/negative evaluations. As a result, he proposed a four-factor model of perceived control⁴, encompassing individuals’ self-evaluations of their ability to (a) avoid negative events (“primary negative control”), (b) cope with negative events (“secondary negative control”), (c) obtain positive events (“primary positive control”) and (d) savour those events (“secondary positive control”). Bryant hypothesized that primary control arises from attitudes regarding behavioural control over aversive or positive events, while secondary control from the strategies individuals use to regulate their own emotions, either by coping with or prolonging them. Thus, while primary control mainly operates on the anticipation of future outcomes, secondary control pertains to the management of prior events.

As we are currently concerned with investigating affect-related animal decision-making, the focus will be directed towards primary control. Therefore, I define dominance as the “conative” quality of affective states. That is, as a parameter related to individual’s inherent drive or inclination as determined by their self-assessed behavioural capacity to obtain positive events and avoid negative ones.⁵ Thus, whereas valence, the hedonic quality of an affective experience, is influenced individuals’ attitudes towards the likelihood of a stimulus being positive or negative, dominance is based on individual’s assessments of their own capability to secure the former and evade the latter. This process spans a spectrum from low to high: individuals can assess themselves as highly or lowly capable of obtaining [avoiding] a positive [negative] outcome. Additionally, I posit that such an assessment can be intrinsically oriented (i.e., an assessment of one’s own capacity to temper with nature) or, on the flipside, externally oriented (i.e., an assessment of whether nature is manageable, also termed “risk-perception”, see Hansson, 2023). Equipped with this definition, I introduce the Valence-Arousal-Dominance (VAD) model and discuss its potential implementation in animal behaviour and welfare research.

4. Dominance and animal decision-making

4.1 The VAD model of affect

I posit that valence (V) represents the magnitude of pleasure experience, arousal (A) signifies the level of physiological activation, and as defined in Section 3.3., dominance (D) encapsulates the degree of behavioural control experienced by the individual within its environment. Due to their relevance in experimental paradigms investigating decision-making, I begin by using the resulting arrangement to characterize moods, that is, diffuse occurrent states that provide information about the type of environment the organism is situated in (Mendl et al., 2005):

⁴ One should pay attention to the use of “perception” in this context, as what is referred to is better described as a kind of attitude.

⁵ Note that, even though individual’s assessment of their own preparedness for their environment may seem to require metacognition, which is typically understood as involving conscious awareness, control and monitoring processes don’t always require awareness.

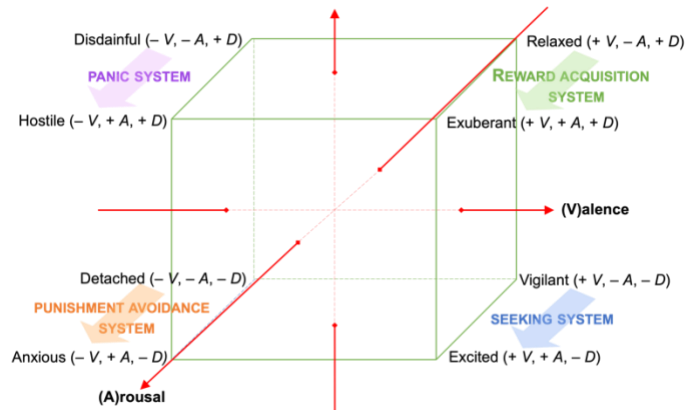


Fig. 5 VAD's model space. The arrows indicate putative biobehavioural systems, including the reward acquisition system (green), the punishment avoidance system (orange), and discrete emotional programs such as SEEKING (blue) and PANIC (purple)

Inspired on Bryant (1990) and Mehrabian (1996), I group moods into the following four classes⁶:

- *High capability of obtaining*: this class comprises the “exuberant” mood (+V, +A, +D), associated with decision-making suited for safe and rewarding events, and the “relaxed” mood (+V, -A, +D) where decisions align with low expectations of non-rewarding, risky events.
- *Low capability of obtaining*: this class includes the “excited” mood (+V, +A, -D), associated with decisions that reflect high expectation of rewarding yet risky events, and the “vigilant” mood (+V, -A, -D), where decisions reflect low expectation of non-rewarding yet safe events.
- *High capability of avoiding*: within this class we find the “hostile” mood (-V, +A, +D), connected with high expectations of encountering non-rewarding but safe events, and the “disdainful” mood (-V, -A, +D), which denotes low expectations of rewarding but risky events.
- *Low capability of avoiding*: lastly, this class includes the “anxious” mood (-V, +A, -D), connected with decisions suited for non-rewarding, risky events, and the “detached” mood (-V, -A, -D), which corresponds to the low expectation of encountering rewarding but safe events.

Furthermore, I posit that individuals do not simply strive for rewarding environments, but rather those that combine rewards and safety and, likewise, that they do not simply avoid non-rewarding environments, but those that are perceived as both non-rewarding and risky. Building upon these premises, I redefine the evolved systems that facilitate such fitness-relevant actions: an individual's position on the (+V, ±A, +D) region, marked by perceived high rewards and low risk, is anticipated to activate the reward-acquisition system (RAS) (cf. the green arrow in figure 5), and an individual's position in the (-V, ±A, -D) region, marked by perceived low rewards and high risk, is anticipated to activate the punishment-avoidance system (PAS) (cf. the orange arrow in figure 5).

In circumstances where individuals perceive situations at once rewarding and punishing (+V, ±A, -D), a question arises regarding the concurrent activation of the RAS and PAS. Such activation might theoretically lead to conflicting behaviours, potentially undermining the functional operationalization of affective states within the proposed model. Alternatively, we may posit that animals, especially those endowed with complex foraging strategies, necessitate the engagement of more specialized affective systems, akin to discrete emotions (refer to section 2.1). Within this hybrid perspective,

⁶ Note that, even though I use some of Mehrabian's (1996) nomenclature (as depicted in figure 4), I characterize the states as belonging to the realm of moods (i.e., long-term diffuse states) rather than personality traits (i.e., stable individual dispositions), which are defined later in this section. Indeed,

dimensional models provide a functional scaffold for the integration of discrete emotions, elucidating their interplay and respective adaptive significance (Panksepp, 2007; Mendl et al., 2010). For instance, while dimensions such as arousal serve overarching psychological functions (e.g., guiding orientation) discrete categories such as anger serve to guide organisms in renewing efforts to achieve desired objectives or overcoming obstructive agents (Harmon-Jones et al., 2017).

Therefore, I propose to associate the (+V, ±A, -D) region with the “SEEKING” and the (-V, ±A, +D) region with the “FEAR” systems (cf. the blue and purple arrows in figure 5, respectively). Originally introduced by Panksepp (1998), these systems coordinate mammals’ adaptative responses to specific environmental challenges. Roughly speaking, SEEKING’s function is to motivate individuals to forage for rewards even though by so doing they expose to risks (Wright and Panksepp, 2012) and FEAR prepares them to escape from punishments, even at the expense of forgoing greater rewards.

Even if their behavioural manifestations may overlap, the activation of the RAS/PAS and SEEKING/FEAR systems may engage different decision-making processes. To wit, within the framework of instrumental reinforcement learning, decision-making can be either “model-free”, when organisms select actions based on their value, or “model-based”, when organisms additionally weight the anticipated outcome of those actions (cf. Mendl & Paul, 2020). Now, Bach and Dayan (2017) observe that model-free decisions can be captured using dimensions such as valence and arousal. In contrast, model-based decisions, by representing actions’ outcomes in a goal-oriented fashion, trigger pre-programmed responses akin to discrete emotions. This suggests that the RAS and PAS would mainly involve model-free decisions while the SEEKING and FEAR systems would comprise model-based decisions. While empirical investigation is required, the V-D plane of the VAD space can be used to characterize them as distinct "macro-systems", illustrated by the dashed arrows in figure 6:

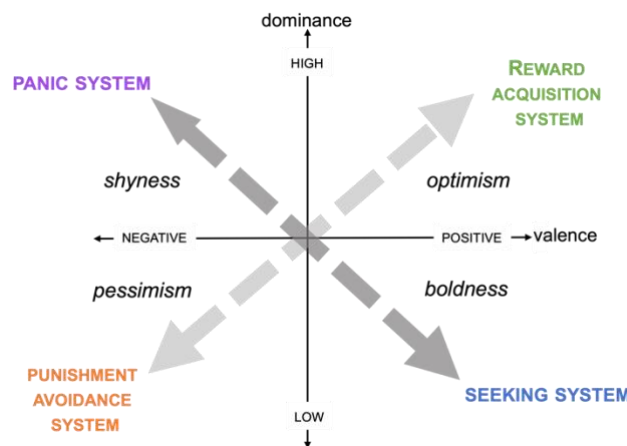


Fig. 6 V-D plane of the VAD’s model space, where the four stipulated biobehavioural systems are hypothesised to constitute extremes within two "macro-systems". The optimist/pessimist and boldness/shyness personalities are located within this plane

Furthermore, I posit that optimism and pessimism are themselves personality traits, i.e., dispositional states that activate under specific conditions, rather than moods, i.e., diffuse occurrent states (e.g., Mendl et al., 2010). This proposal is grounded on empirical evidence suggesting that an individual’s level of optimism tends to be a relatively stable trait not entirely explicable by genotype, environment, or genotype-by-environment interactions (Bračić et al., 2022). One advantage of this perspective is that, unlike moods, personality continua are not mutually exclusive. Since personalities are

dispositional states, individuals can be potentially aggressive and friendly given that certain conditions are met, for example. Thus, the model allows the possibility that members of a particular species may exhibit boldness traits despite having pessimist expectations or shyness traits despite being optimist. Empirically testing such assumption would shed light on the relation between the boldness-shyness and the optimism-pessimism continua, which I as follow:⁷

- Individual behavioural responses are qualified as “optimistic” or “pessimistic”, I assume, not only based on the perceived valence of an outcome but also on its perceived safety. These personality traits are particularly relevant in situations where incoming sensory information is ambiguous and yet individual’s survival depends on taking an optimal decision. Accordingly, individuals that show enhanced expectations of (+V, +D) events (i.e., that tend to be in an “exuberant” or “relaxed” mood) are optimist, and those that show enhanced expectations of (−V, −D) events (i.e., that tend to be in an “anxious” or “detached” mood) are pessimist (see figure 6).
- Individual behavioural responses are qualified as “shy” or “bold”, I contend, based on different assessments of reward and safety trade-offs, that is, by considering whether potential benefits outweigh risks or vice versa. These personality traits are more useful in cases where the sensory input requires the evaluation and integration of multiple factors. Accordingly, individuals that tend to favour (+V, −D) events (i.e., that tend to be in a “vigilant” or “excited” mood) are bold, and conversely, those that tend to favour (−V, +D) events (i.e., that tend to be in a “hostile” or “disdainful” mood) are shy (see figure 6).

Before moving on, it is worth noting that when analysing animals’ affective responses, the absence of an overt behavioural outcome may, but does not need to, indicate low levels of arousal. Indeed, heightened arousal manifest not only through active instrumental responses such as approaching or avoiding but also through freezing (Gray & McNaughton, 2000). Therefore, I characterize the midpoint of the V-D plane as a “paralysis point”, which denotes scenarios where none of the available actions (or outcomes thereof) appear favourable, thus leading to an absence of clear behavioural responses despite heightened arousal levels. With this theoretical framework in place, we can proceed to explore the research avenues that the VAD model offers. To establish a contextual foundation for the application of the VAD model, I will briefly introduce how functional operationalizations of affect are standardly used within Judgment Bias Tests.

4.2 The Judgment Bias Test

The Judgment Bias Test studies animal decision-making biases under conditions of ambiguity (Harding et al., 2004; Bethell, 2015; Nguyen et al., 2020), grounded on evidence that individuals undergoing negative states tend to manifest more pronounced “pessimistic” judgments relative to their counterparts in more positive states. In this section, I briefly present the main design principles of the JBT and, in the following, propose areas where the VAD model can expand the findings of the JBT paradigm. As depicted in figure 7, the test typically comprises the following three phases:

- A. During the **training phase**, animals are presented with "positive" cues, which result in a reward, and "negative" cues, which result in a relatively smaller reward or punishment (e.g., white noise). Through repeated trial and error, animals learn to respond positively by approaching the reward-associated stimulus and to respond negatively by avoiding the punishment-associated stimulus, that is, by activating the RAS and PAS.

⁷ Even though animal personality traits are not typically discussed in relation to emotions within behavioural ecology, research in human psychology underscores the value of studying individual differences in emotions and moods as means to shed light into the dynamics of personalities (or “temperament”) in a bottom-up fashion, particularly in relation to welfare and psychopathologies (e.g., Montag & Panksepp, 2017).

- B. In the **testing phase**, animals are periodically exposed to cues which are qualitatively “ambiguous” with respect to the training positive and negative cues (e.g., sounds of intermediate frequency with respect to training cues). Importantly, the behavioural responses to the ambiguous cues are considered indicative of animals’ anticipations of positive or negative outcomes, operationalized as “optimistic” or “pessimistic” biases (even though other factors, such as sensitivity to reinforcement, are also likely to be involved in these decisions, see Lecorps et al., 2021).
- C. Lastly, in the **priming phase**, a subset of animals undergoes a treatment intended to alter their affective state either positively (e.g., clean bedding) or negatively (e.g., unpredictable housing) before the testing phase, while the other animals serve as the control group.

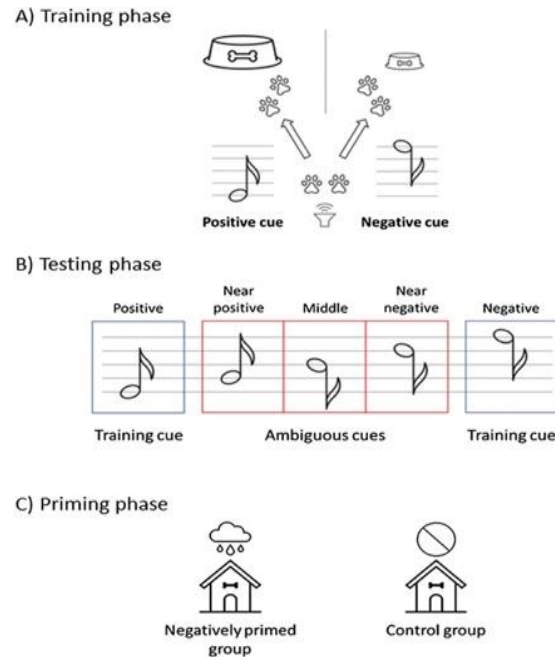


Fig. 7 Example of the JBT design in Nematipour et al. (2022), representing A) the training phase, where animals are presented with low and high-pitched tones; B) the testing phase, where animals are also presented with pitches intermediate to the training tones; and C) the priming phase, where a subgroup of the animals is exposed to unpredictable housing to induce a negative state

The outcomes of a JBT with negative priming can yield the following results. First, animals from the negatively primed group may exhibit a pessimistic bias by responding more often in the negative way to the ambiguous cues compared to the animals from the control group. This outcome either validates the testing paradigm by demonstrating its ability to detect changes in affective states or provides evidence that the applied priming manipulation indeed altered the animals’ emotional state. Second, animals from the negatively primed group may display a positive judgment bias by responding more frequently in the positive way to the ambiguous cues (and vice versa for the positively primed group). Without additional information about the animals’ cognitive abilities and the contextual factors potentially influencing their behaviour, a definite interpretation of this result cannot be provided. Third, priming may not result in a statistically significant difference between the treatment and control groups. This may suggest that the priming did not elicit a lasting emotional state or that the bias is too subtle to be detected under the chosen experimental conditions.

4.3 The Environment Choice Test and beyond

The JBT measures behavioural responses to experimental conditions possessing the potential for either reward or punishment, i.e., that can elicit positive or negative states. However, ecologically relevant situations present stimuli that intertwine both features. To understand animal’s decision-making with respect to this kind of situations, I refer to the work of Bračić et al. (currently under review), a proof-of-principle experiment that highlights some of the limitations of the JBT. In this section, I argue that Bračić et al. study serves as a notable example of how the VAD model can be effectively applied.

The authors highlight the need to test the potential ecological relevance of optimism and pessimism. To that effect, they introduce a novel testing protocol named the “Environment Choice Test” (ECT), designed to explore foraging decision-making under predation risk. Their study is composed of two experimental phases. The initial one involves the JBT, wherein laboratory mice are presented with ambiguous cues to assess their level of optimism, quantified as “optimism score”. In the second, the study incorporates the ECT, where mice are confronted with a choice between two chambers connected by short tunnels: a) the “predator chamber”, laden with predator cues (rat odour or illumination) but yielding a substantial reward and b) “the safe chamber”, containing clean bedding yet yielding a small reward (see figure 8). The mice’s decision-making rates are quantified as “choice score”.⁸

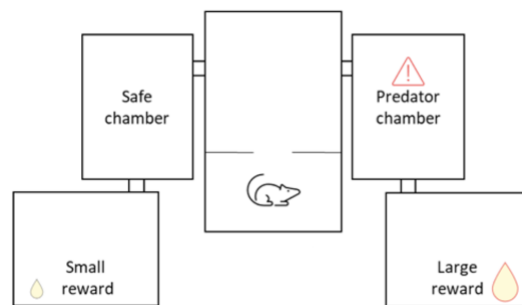


Fig. 8 Environment Choice Test (Bračić et al., under review). The test apparatus consists of five interconnected chambers. On each side, there are cue chambers where predator cues (“predator chamber”) or clean bedding (“safe chamber”) are introduced. During the test, mice need to traverse one of these chambers to finally reach a reward: by going through the predator chamber, they could claim a large reward and through a safe chamber, a small reward

The authors found that mice express consistent differences in their choices of the predator or safe chamber. Yet, they found no correlation between mice’s individual optimism and choice score, suggesting that optimists, although expecting positive outcomes, might not take more risks when it can jeopardize their survival. The authors discuss the possibility that these results may be due to the functioning of distinct or similar underlying cognitive mechanisms which are, however, differently affected by previous life experiences.

As the ECT compels animals to strike a balance between avoiding predation exposure and capitalizing on foraging opportunities, the VAD offers a framework for interpreting its results through the lens of affective dimensions. To begin with, by juxtaposing conditions of small and large rewards with those of low and high risk, the predator and safe chambers can be characterized as the (+V, -D) and the (-V, +D) conditions, respectively. Consequently, as per the definition of personalities outlined in Section 4.1, consistent reactions to these cues can be construed as reflecting individuals’ personalities:

⁸ Note that, during the pre-training session, mice discovered that one side of the apparatus contains a large reward while other contains a small reward and learned how to reach them. When their accuracy reached 80%, they proceeded to the test.

mice are bold when favouring the predator chamber and shy when evincing a predilection for the safe chamber. Aggregating these decisions can thus be quantified as a “boldness score”.⁹

As we saw in section 4.1, the VAD model posits that optimistic and boldness personalities engage distinct macro-behavioural systems. Specifically, the RAS/PAS and the SEEKING/FEAR systems, respectively (cf. figure 6). As these macro-systems are probably involved in different types of decision-making (i.e., model-free in the former case vs. model-based in the latter), the model predicts absence of correlation between optimistic and boldness personalities. Bračić et al.’s finding that optimism and choice (i.e., boldness) scores don’t correlate can be interpreted as substantiating such prediction, or at least confirming the VAD model’s assumption that multiple personalities may co-exist within the same individual (thus creating “behavioural syndromes”; see Sih et al., 2004).

Lastly, the VAD model also bears the potential to assist in further supporting research that involves probing the influence of individual’s state on risk-taking. To wit, there is considerable evidence indicating that animals’ health (Heithaus et al., 2007), nutrition (reviewed in Moran et al., 2020), and stress (Sih, 2011) markedly influences their propensity for risk-taking (however, see Niemelä & Dingemans, 2018). Heithaus et al. (2007) study, for example, suggests that the health of green-sea turtles modulates their trade-off between food and safety. In a mechanistic study of this kind, one can, for example, measure the choice (boldness) score of individual mice, following Bračić et al.’s (under review) paradigm, induce stressors or other treatments on a randomly selected sub-group thereof, and then track whether and to what extent treatments make individuals shyer or bolder.

In this context, the advantage of conducting a behavioural study against the background of the VAD model extends beyond its capacity to generate translatable hypotheses pertaining to the scenarios that elicit affective states and the expected responses of animals. It also elucidates shared patterns among seemingly disparate phenomena. To wit, even though the optimistic-pessimist continuum has been functionally defined (using affective dimensions) as individual’s expectations of positive or negative outcomes, the shyness-boldness continuum typically escaped such mapping. Thus, by unifying them under a multidimensional framework of affect, and locating them in the realm of personality traits, we can achieve a more complete picture of the structure of animal affect (for insights into the unifying role of explanations, see Kitcher, 1981). Moreover, empirical research in the field of animal behaviour can, in turn, iteratively enhance the precision of the operational definitions of affective phenomena within the VAD model, thus establishing a solid foundation for the development of a theory of animal affect (Moors, 2022).

As explored in this section, the VAD model provides a platform to examine personality-modulated decision-making through manipulative experiments. That is, by studying how affective responses to adverse or favourable living conditions precipitate cognitive shifts that may impact an animal’s foraging strategies. However, as we will discuss in the next section, dominance can also help us to look at living conditions beyond the presence of rewards or punishments.

5. Discussion

5.1 Dominance and animal welfare

Discussions of positive states are relatively scarce in psychology, as research on states such as joy or love have often overlooked delineating their behavioural or physiological aspects (with exceptions,

⁹ The boldness score can be considered to give a snapshot of the personality of an individual relative to that of other members of its group within the particular within a particular temporal frame, delineating inter-individual variation. However, given the stable character of personality traits, repeated testing individuals is necessary to see whether individuals consistently exhibit bolder or shyer tendencies, constituting intra-individual variation.

e.g., Fredrickson, 2001).¹⁰ Similarly, animal welfare science has, until the beginning of the millennium, predominantly focused on how to avoid and assess negatively valenced experiences including stress and pain. However, the study of positive experiences has more recently gained momentum (Mellor, 2012), based on a “desire to describe the conditions under which the animals thrive, not simply survive” (Hintze, 2022, p. 795).

However, positive experiences defy straightforward characterizations and measurement. In human psychology, it is considered that happiness can be achieved either by obtaining extrinsically rewarding outcomes, or else by the pursuit of an activity that is rewarding irrespective of any end-product, such as playing (White, 1959; Becker et al., 2019). Even though the latter pursuit is considered to enhance well-being to a greater extent (Sheldon & Kasser, 1998), there are relatively few studies with animals targeting intrinsic motivation. In this section, I argue that the dominance dimension not only holds the potential to refine measurements and explanations regarding animal decision-making, but also regarding happiness-inducing living conditions.

A concept that drives the study of intrinsic motivation and well-being is “flow” (Csikzentmihalyi, 1990; Csikzentmihalyi, 2002; Hintze, 2022). Flow is defined as a state of complete absorption in an autotelic activity that requires constructing a dynamic balance between an individual’s perceived skills and the degree of challenge presented by the activity. To put it differently, flow requires that the demands of the task are maintained within a manageable scope without being totally predictive of the outcome. This balance is thus not static but unfolds throughout an activity by applying effort to a series of attainable goals, processing feedback regarding progress, and adapting action based on this feedback.

Crucially, satisfaction from an autotelic activity seems to be determined by a continuous equilibrium between the sensation of one’s own capacity to temper with nature and the challenges it imposes. Consequently, I propose to conceive valence as mainly modulated by the acquisition of rewards such as food or shelter, and dominance as modulated by the success in overcoming environmental challenges. In both cases, it is likely that long-term imbalances carry drawbacks. In humans, for example, excessive abundance of resources has been observed to foster inertia, while scarcity of resources is correlated with depressive and anxiety disorders. Similarly, surmounting each challenge generates dullness, while failing to do so results in frustration (Csikszentmihalyi, 1990). Thus, drawing inspiration from Bakker et al. (2014), I illustrate the landscape of affective harmony as follows¹¹:

¹⁰ Thanks to [...] for drawing my attention to this aspect.

¹¹ It is crucial to clarify that while flow serves as an intriguing benchmark for understanding well-being, it represents a somewhat unique and relatively infrequent state of optimal experience. Not all experiences or situations aim to induce a flow state in animals. Rather, we introduce the concept of flow in the context of animal welfare to highlight the potential for animals to experience moments of optimal engagement and fulfillment. However, we recognize that animal welfare science encompasses various perspectives and approaches, and our model's value extends beyond any specific position, making it potentially useful for a range of applications within the field.

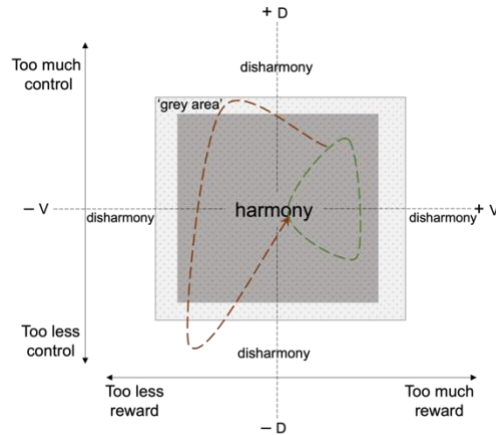


Fig. 9 Harmony space. The levels of reward and control serve as indicators of harmony and disharmony in an animal's perceived environment. The green and red dashed lines indicate hypothetical scenarios of an organism's affective states fluctuating over time. The green line represents cycles characterized by successful competition for rewards, whereas the red lines represent cycles marked by unsuccessful competition

The grey area denotes the experience of harmony, while the area outside it represents disharmony. Well-being hinges on a balanced interplay between excess or insufficiency of extrinsic rewards, as well as between perceived skills and environmental challenges. In line with Mendl et al. (2010), this space allows us to chart an organism's evolving affective trajectory within its environment, as driven by the moods it undergoes. In group foraging, for example, initially discovering of a prey in an easily accessible location may elicit cycles of exuberance (+V, +D) and then excitement (+V, -D), due to the competition for this resource from other group members, as depicted by the green dashed line in figure 9. However, as depicted by the red dotted line, this cycle could be interrupted by a cycle where losing access to the shared reward may generate anxiety (-V, -D) or hostility (-V, -D). Insofar as green and red cycles don't become too intense or frequent, they can be considered to constitute a harmonious experience.

Expanding on this insight, the extended Environment Choice Test can be improved. As proposed in section 4.3, after applying the ECT we can randomly divide mice into two groups, exposing them to either positive or negative enrichments. However, instead of concentrating around provisions like shelter and food, the potential for cognitive stimulation through flow induction can be explored (Clark, 2017). Therefore, we could induce animals to experience varying degrees of equilibrium and disequilibrium in the interplay between their skills and environmental challenges. In this case, disequilibrium can be obtained either by making challenges either too easy or too difficult. For instance, artificial prey moved on a rope to stimulate hunting can have its challenge level modified by altering one parameter such as the speed or by introducing unpredictable movements.¹²

To ascertain whether flow has been effectively induced, researchers can assess animal's resistance to increasingly attractive external distractions. However, the design principles of flow inducing tasks and their integration to the extended ECT should be deduced by considering the species' ecological niche and the typical challenges it confronts. To end this paper, these details will be briefly discussed in the next section.

¹² As a prospective avenue, which I leave for future exploration, the link between dominance and well-being could be studied through an inquiry of dominance as secondary control, i.e., of animal's capacity to adjust their internal states to occurring or past events (see section 3.3).

5.2 Some logistic considerations¹³

Symmetry of Payoffs. It has been observed that the standard JBT requires that the perceived payoff of the negative and the positive outcomes should be symmetrical: if the perceived negative value of the punishment (e.g., electricity shock) is much stronger than the perceived positive value of a food pellet, animals would be strongly motivated to avoid the former stimulus (Lagisz et al., 2020). In the ECT, where stimuli combine level of reward and punishment, this requirement becomes crucial. To wit, ensuring that the absolute value of the predator chamber and safe chamber are similar prevents skewed motivation towards one stimulus over the other. However, a solution is to talk about personality traits not in terms of stable behavioural dispositions (e.g., as animals being consistently risk-seeking) but only in terms of behavioural differences between individuals within a group (e.g., as being more risk-seeking than other individuals), thus establishing a rank order that is independent of how the values of the rewards and punishment change.

Animal selection and training. Selecting and training animals meticulously is paramount. In particular, choosing animals above a certain threshold of shyness seems to be crucial for meaningful results, as subjecting extremely shy organisms to long training sessions may not effectively indicate the impact of negative or positive priming on their decision-making. However, on the other hand, a problem can occur if only those animals that can manage the task within a reasonable time window are selected in a study, as that may entail choosing animals with a particular personality type.

Distinguishing Biobehavioural Systems. In section 4.1, we distinguished the SEEKING/FEAR from the PAS/RAS in terms of their cognitive underpinnings. However, it remains plausible that they are also distinguished in the complexity of their behavioural outcomes. Yet, discerning which system is being used by looking at behavioural responses alone presents various challenges, such as designing tools to distinguish between different types of approaching and avoidance. More importantly, not all animals can be considered to have those specialized systems, but probably mammals with complex foraging strategies. Another possibility, that hasn't been explored in this paper, is that the PAS and RAS compete by mutually influencing each other and therefore generate a "higher level" bi-polar dimension (Leknes & Tracey, 2008), akin to dominance.

6. Conclusion

Research across species underscores that animals can be sophisticated evaluators of the quality of their environment, for example, by weighing multiple factors to take critical decisions in the face of danger. Dominance emerges as a pivotal mediator in this intricate decision-making process, exerting a profound role on the core of an animal's personality and subsequent moods. While the optimism-pessimism and the boldness-shyness continua have been standardly examined in isolation, our three-dimensional model allows for a framework where tractable hypotheses about their potential positive or negative correlation across species can be formulated. These personality traits, the VAD model assumes, plausibly invoke distinctive biobehavioural systems, involving either model-free or model-based decision-making. As such, they furnish animals with the adaptive flexibility requisite for responding effectively to the different challenges presented by their environment. As we move forward, future research should aim to empirically test and refine this, as well as further extensions of valence-arousal models, while also exploring the applicability of dominance to other facets of animals' lives, such as the expression of their affective states. Importantly, the methodologies potentially employed in studying dominance in animals, especially concerning well-being and flow states, open the discussion about the extent to which findings within animal affect research can be translated to human affect research.

¹³ Thanks to [...] for their suggestions on this section.

Bibliography

- Bach, D.R. and Dayan, P. (2017). Algorithms for survival: a comparative perspective on emotions. *Nature Reviews Neuroscience*, 18(5), pp. 311-319. <http://dx.doi.org/10.1038/nrn.2017.35>
- Bakker, I., Van Der Voordt, T., Vink, P., & De Boon, J. (2014). Pleasure, arousal, dominance: Mehrabian and Russell revisited. *Current Psychology*, 33, 405-421. <https://doi.org/10.1007/s12144-014-9219-4>
- Barrett, L.F. (2017). *How emotions are made: The secret life of the brain*. Pan Macmillan.
- Becker, S., Bräscher, A.K., Bannister, S., Bensafi, M., Calma-Birling, D., Chan, R.C., Eerola, T., Ellingsen, D.M., Ferdenzi, C., Hanson, J.L. and Joffily, M. (2019). The role of hedonics in the Human Affectome. *Neuroscience & Biobehavioral Reviews*, 102, pp.221-241. <http://dx.doi.org/10.1016/j.neubiorev.2019.05.003>
- Bleicher, S. S. (2017). The landscape of fear conceptual framework: definition and review of current applications and misuses. *PeerJ*, 5. <https://doi.org/10.7717/peerj.3772>
- Bradley, M.M., Greenwald, M.K., Petry, M.C. and Lang, P.J. (1992). Remembering pictures: pleasure and arousal in memory. *Journal of experimental psychology: Learning, Memory, and Cognition*, 18(2), p.379. <https://doi.org/10.1037//0278-7393.18.2.379>
- Bračić, M., Bohn, L., Siewert, V., von Kortzfleisch, V.T., Schielzeth, H., Kaiser, S., Sachser, N. and Richter, S.H. (2022). Once an optimist, always an optimist? Studying cognitive judgment bias in mice. *Behavioral Ecology*, 33(4), pp.775-788. <https://doi.org/10.1093/beheco/arac040>
- Bračić M., Bierbaum L., Peng M., Nimalavachchlan L., Siewert V., Kaiser S., Sachser N., Richter H. (under review). The behavioural ecology of optimism: exploring potential consequences of judgement bias in mice. <https://doi.org/10.17605/OSF.IO/Z6NM8>
- Bryant, F.B. (1989). A four-factor model of perceived control: Avoiding, coping, obtaining, and savoring. *Journal of personality*, 57(4), pp.773-797. <https://doi.org/10.1111/j.1467-6494.1989.tb00494.x>
- Carver, C. S., & Harmon-Jones, E. (2009). Anger is an approach-related affect: evidence and implications. *Psychological bulletin*, 135(2), 183. <https://doi.org/10.1037/a0013965>.
- Clark, F.E. (2017). Cognitive enrichment and welfare: Current approaches and future directions. *Anim. Behav. Cogn.* 4(1), pp.52-71. <https://doi.org/10.12966/abc.05.02.2017>
- Csikszentmihalyi, M. (1990). *Flow: The Psychology of Optimal Experience*. Harper and Row, New York.
- Csikszentmihalyi, M. (2002). *Flow: The Classic Work on How to Achieve Happiness*. Random House, London.
- Deonna, J. and Teroni, F. (2012). *The emotions: A philosophical introduction*. Routledge.
- De Sousa, R. (2003). Emotion. *Stanford Encyclopedia of Philosophy*, 3.
- Ekman, P. (1984). Expression and the nature of emotion. *Approaches to emotion*, 3(19), 344.
- Ellsworth, Phoebe C., and Scherer, K. R. (2003), Appraisal Processes in Emotion, in Richard J. Davidson, Klaus R. Scherer, and H. Hill Goldsmith (eds.), *Handbook of Affective Sciences*, Oxford: Oxford University Press, 572–595.
- Fontaine, J.R., Scherer, K.R., Roesch, E.B. and Ellsworth, P.C. (2007). The world of emotions is not two-dimensional. *Psychological science*, 18(12), pp.1050-1057. <https://doi.org/10.1111/j.1467-9280.2007.02024.x>
- Fredrickson, B.L. (2001). The role of positive emotions in positive psychology: The broaden-and-build theory of positive emotions. *American psychologist*, 56(3), p.218. <https://doi.org/10.1037//0003-066x.56.3.218>
- Frigg, R. and Hartmann S. (2020), "Models in Science", *The Stanford Encyclopedia of Philosophy* (Spring 2020 Edition), Edward N. Zalta (ed.).
- Frijda, N. (1994). Emotions are functional, most of the time. In: Ekman, P., Davidson, R.J. (eds.), *The Nature of Emotion: Fundamental Questions*. Oxford University Press, Oxford, pp. 112–122.
- Gray J.A., McNaughton N. (2000). *The neuropsychology of anxiety: An enquiry into the function of the septo-hippocampal system*. Oxford: Oxford University Press.
- Gregory, W.L. (1978). Locus of control for positive and negative outcomes. *Journal of Personality and Social Psychology*, 36(8), p. 840. <https://doi.org/10.1037/0022-3514.36.8.840>
- Hansson, S. O. (2023), "Risk", *The Stanford Encyclopedia of Philosophy* (Summer 2023 Edition), Edward N. Zalta & Uri Nodelman (eds.)
- Harding, E.J., Paul, E.S. and Mendl, M. (2004). Cognitive bias and affective state. *Nature*, 427(6972), pp.312-312. <https://doi.org/10.1038/427312a>
- Harmon-Jones, E., Harmon-Jones, C. and Summerell, E. (2017). On the importance of both dimensional and discrete models of emotion. *Behavioral sciences*, 7(4), p.66. <https://doi.org/10.3390/bs7040066>
- Heithaus, M.R., Frid, A., Wirsing, A.J., Dill, L.M., Fourqurean, J.W., Burkholder, D., Thomson, J. and Bejder, L. (2007). State-dependent risk-taking by green sea turtles mediates top-down effects of tiger shark

intimidation in a marine ecosystem. *Journal of Animal Ecology*, 76(5), pp.837-844. <https://doi.org/10.1111/j.1365-2656.2007.01260.x>

Hintze, S. and Yee, J.R. (2023). Animals in flow—towards the scientific study of intrinsic reward in animals. *Biological Reviews*, 98(3), pp.792-806. <https://doi.org/10.1111/brv.12930>

Kaiser, M.I. and Müller, C. (2021). What is an animal personality?. *Biology & Philosophy*, 36(1), p.1.
Kitcher, P. (1981). Explanatory unification. *Philosophy of science*, 48(4), pp.507-531.

<https://doi.org/10.1007/s10539-020-09776-w>

Kremer, S.E.J. Klein Holkenborg, I. Reimert, J.E. Bolhuis, L.E. Webb (2020). The nuts and bolts of animal emotion, *Neuroscience & Biobehavioral Reviews*, Volume 113, Pages 273-286.

<https://doi.org/10.1016/j.neubiorev.2020.01.028>

Lagisz, M., Zidar, J., Nakagawa, S., Neville, V., Sorato, E., Paul, E.S., Bateson, M., Mendl, M. and Løvlie, H. (2020). Optimism, pessimism and judgement bias in animals: a systematic review and meta-analysis. *Neuroscience & Biobehavioral Reviews*, 118, pp.3-17. <https://doi.org/10.1016/j.neubiorev.2020.07.012>

Laskowski, K.L., Chang, C.C., Sheehy, K. and Aguiñaga, J. (2022). Consistent individual behavioral variation: what do we know and where are we going?. *Annual Review of Ecology, Evolution, and Systematics*, 53, pp.161-182. <https://doi.org/10.1146/annurev-ecolsys-102220-011451>

LeDoux, J. E. (2022). As soon as there was life, there was danger: the deep history of survival behaviours and the shallower history of consciousness. *Phil. Trans. R. Soc. B.* <http://doi.org/10.1098/rstb.2021.0292>

Lecorps, B., Weary, D.M. and von Keyserlingk, M.A. (2021). Negative expectations and vulnerability to stressors in animals. *Neuroscience & Biobehavioral Reviews*, 130, pp.240-251.

<https://doi.org/10.1016/j.neubiorev.2021.08.025>

Leknes, S. and Tracey, I. (2008). A common neurobiology for pain and pleasure. *Nature reviews neuroscience*, 9(4), pp. 314-320. <https://doi.org/10.1038/nrn2333>

Lerner, J. S., & Keltner, D. (2001). Fear, anger, and risk. *Journal of Personality and Social Psychology*, 81(1), 146–159. <https://doi.org/10.1037/0022-3514.81.1.146>

Mehrabian, A. and Russell, J.A. (1974). *An approach to environmental psychology*. The MIT Press.

Mehrabian, A. (1996). Pleasure-arousal-dominance: A general framework for describing and measuring individual differences in temperament. *Current Psychology*, 14, 261-292. <https://doi.org/10.1007/BF02686918>

Mellor, D.J. (2012). Animal emotions, behaviour and the promotion of positive welfare states. *New Zealand veterinary journal*, 60(1), pp.1-8. <https://doi.org/10.1080/00480169.2011.619047>

Mellor, D.J. (2016) Updating Animal Welfare Thinking: Moving beyond the “Five Freedoms” towards “A Life Worth Living”. *Animals*, 6, 21. <https://doi.org/10.3390/ani6030021>

Mendl, M., Burman, O. H., & Paul, E. S. (2010). An integrative and functional framework for the study of animal emotion and mood. *Proceedings of the Royal Society B: Biological Sciences*, 277(1696), 2895-2904. <https://doi.org/10.1098/rspb.2010.0303>

Mendl, M. and Paul, E.S. (2020). Animal affect and decision-making. *Neuroscience & Biobehavioral Reviews*, 112, pp.144-163. <https://doi.org/10.1016/j.neubiorev.2020.01.025>

Montag, C. and Panksepp, J. (2017). Primary emotional systems and personality: an evolutionary perspective. *Frontiers in psychology*, 8, p.464. <https://doi.org/10.3389/fpsyg.2017.00464>

Moors, A. (2013). On the Causal Role of Appraisal in Emotion, *Emotion Review*, 5(2): 132–140. <https://doi.org/doi:10.1177/1754073912463601>

Moors, A. (2022). *Demystifying emotions: A typology of theories in psychology and philosophy*. Cambridge University Press.

Moran, N.P., Sánchez-Tójar, A., Schielzeth, H. and Reinhold, K. (2021). Poor nutritional condition promotes high-risk behaviours: A systematic review and meta-analysis. *Biological Reviews*, 96(1), pp.269-288. <https://doi.org/10.1111/brv.12655>

Nematipour, B., Bračić, M., & Krohs, U. (2022). Cognitive bias in animal behavior science: A philosophical perspective. *Animal Cognition*, 25(4), 975-990. <https://doi.org/10.1007/s10071-022-01647-z>

Neethirajan, S., Reimert, I., & Kemp, B. (2021, January 14). Measuring Farm Animal Emotions—Sensor-Based Approaches. <https://scite.ai/reports/10.3390/s21020553>

Niemelä, P.T. and Dingemanse, N.J. (2018). Meta-analysis reveals weak associations between intrinsic state and personality. *Proceedings of the Royal Society B: Biological Sciences*, 285(1873), p.20172823. <https://doi.org/10.1098/rspb.2017.2823>

Osgood, C. E. (1966). Dimensionality of the semantic space for communication via facial expressions. *Scandinavian journal of psychology*, 7(1), 1-30. <https://doi.org/10.1111/j.1467-9450.1966.tb01334.x>

- Oosterhof, N. N., & Todorov, A. (2008). The functional basis of face evaluation. *Proceedings of the National Academy of Sciences*, 105(32), 11087-11092. <https://doi.org/10.1073/pnas.0805664105>
- Panksepp, J. (1998). *Affective neuroscience: The foundations of human and animal emotions*. Oxford university press.
- Panksepp, J. (2007). Neurologizing the psychology of affects: How appraisal-based constructivism and basic emotion theory can coexist. *Perspectives on psychological science*, 2(3), pp.281-296. <https://doi.org/10.1111/j.1745-6916.2007.00045.x>
- Paul, E.S., Harding, E.J. and Mendl, M. (2005). Measuring emotional processes in animals: the utility of a cognitive approach. *Neuroscience & Biobehavioral Reviews*, 29(3), pp.469-491. <https://doi.org/10.1016/j.neubiorev.2005.01.002>
- Réale, D., Reader, S.M., Sol, D., McDougall, P.T. and Dingemans, N.J. (2007). Integrating animal temperament within ecology and evolution. *Biological reviews*, 82(2), pp.291-318. <https://doi.org/10.1111/j.1469-185X.2007.00010.x>
- Rolls, E. T. (2005). *Emotion Explained* (Series in Affective Science). UK: Oxford University Press.
- Rothbaum, F., Weisz, J.R. and Snyder, S.S. (1982). Changing the world and changing the self: A two-process model of perceived control. *Journal of personality and social psychology*, 42(1), p.5. <https://doi.org/10.1037/0022-3514.42.1.5>
- Russell, J. A., & Mehrabian, A. (1977). Evidence for a three-factor theory of emotions. *Journal of research in Personality*, 11(3), 273-294. [https://doi.org/10.1016/0092-6566\(77\)90037-X](https://doi.org/10.1016/0092-6566(77)90037-X)
- Russell, J. A. (1978). Evidence of convergent validity on the dimensions of affect. *Journal of personality and social psychology*, 36(10), 1152. <https://doi.org/10.1037/0022-3514.36.10.1152>
- Russell, J. A. (1980). A circumplex model of affect. *Journal of personality and social psychology*, 39(6), 1161. <https://doi.org/10.1017/S0954579405050340>
- Russell, J. A., & Barrett, L. F. (1998). Core affect, prototypical emotional episodes, and other things called emotion: dissecting the elephant. *Journal of personality and social psychology*, 76(5), 805. <https://doi.org/10.1037//0022-3514.76.5.805>
- Scherer, K.R. (2005). What are emotions? And how can they be measured?. *Social science information*, 44(4), pp.695-729. <https://doi.org/10.1177/0539018405058216>
- Scherer, K.R. (2009), "The Dynamic Architecture of Emotion: Evidence for the Component Process Model", *Cognition and Emotion*, 23(7): 1307–1351. <https://doi.org/doi:10.1080/02699930902928969>
- Schiller, D., Yu, A. N. C., Alia-Klein, N., Becker, S., Cromwell, H. C., Dolcos, F., ... Lowe, L. (2022, June 11). The Human Affectome. <https://doi.org/10.31234/osf.io/9nu32>
- Sheldon, K.M. and Kasser, T. (1998). Pursuing personal goals: Skills enable progress, but not all progress is beneficial. *Personality and social psychology bulletin*, 24(12), pp.1319-1331. <https://doi.org/10.1177/01461672982412006>
- Sih, A., Bell, A. and Johnson, J.C. (2004). Behavioral syndromes: an ecological and evolutionary overview. *Trends in ecology & evolution*, 19(7), pp.372-378. <https://doi.org/10.1016/j.tree.2004.04.009>
- Sih, A. (2011). Effects of early stress on behavioral syndromes: an integrated adaptive perspective. *Neuroscience & Biobehavioral Reviews*, 35(7), pp.1452-1465. <https://doi.org/10.1016/j.neubiorev.2011.03.015>
- Uexküll, J.B. (1934). *Streifzüge durch die Umwelten von Tieren und Menschen Ein Bilderbuch unsichtbarer Welten*: Einundzwanzigster Band.
- Watson, D., & Tellegen, A. (1985). Toward a consensual structure of mood. *Psychological Bulletin*, 98(2), 219–235. <https://doi.org/10.1037/0033-2909.98.2.219>
- Watson, D., Wiese, D., Vaidya, J. and Tellegen, A. (1999). The two general activation systems of affect: Structural findings, evolutionary considerations, and psychobiological evidence. *Journal of personality and social psychology*, 76(5), p.820. <https://doi.org/10.1037/0022-3514.76.5.820>
- Webber, S., Cobb, M., & Coe, J. C. (2022, June 30). Welfare Through Competence: A Framework for Animal-Centric Technology Design. <https://scite.ai/reports/10.3389/fvets.2022.885973>
- White, R.W. (1959). Motivation reconsidered: the concept of competence. *Psychological review*, 66(5), p.297. <https://doi.org/10.1037/h0040934>
- Wright, J.S. and Panksepp, J. (2012). An evolutionary framework to understand foraging, wanting, and desire: the neuropsychology of the SEEKING system. *Neuropsychanalysis*, 14(1), pp.5-39. <https://doi.org/10.1080/15294145.2012.10773683>
- Zachar, P. and Ellis, R.D. eds. (2012). *Categorical versus dimensional models of affect: a seminar on the theories of Panksepp and Russell* (Vol. 7). John Benjamins Publishing.