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

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Abstract

This paper critically examines the philosophical underpinnings of current experimental investigation into animal affect-related decision-making. A standard assumption in the operationalization of affective states associates the activation of positively valenced states with approach behaviours and of negatively valenced states with avoidance behaviours. While this assumption provides a useful starting point, its constraints become apparent in light of evidence of instances where valenced and motivational states do not neatly align, namely, cases where "wanting" does not entail "liking". To address this limitation, this paper proposes the (re-)integration of *dominance* as a dimension of affect. In particular, I argue that dominance, construed as a measure of organisms' self-assessed behavioural control, can provide the necessary nuance to understand how animals navigate environmental challenges. Then, following the examination of theoretical and methodological challenges related to incorporating dominance into a definition of affective states, this paper introduces the "Valence-Arousal-Dominance" model of affect. The model is explored for its potential applications in two domains: firstly, in the investigation of animal affect-related decision-making under predation risk, and secondly, in the study of animal wellbeing. Through these applications, this model aims to bring experimental paradigms of animal affect-related behaviour closer to ecologically relevant scenarios.
Keywords: emotion – dominance – judgment bias – decision-making – core affect

1 Introduction

Affective states, such as emotions and moods, constitute a thriving area of research within the field of non-human animal (henceforth "animal") behavioural biology (see, e.g., Mellor, 2016; Mendl & Paul, 2020; Neethirajan et al., 2021). This interest stems from the increasing evidence indicating that positively and negatively valenced affective states can exert a pivotal influence on animals' cognitive landscape and wellbeing (Webber et al., 2022). Despite standard scepticism regarding the explanatory value of affective states in ethological research (see the review in Burghardt, 2019), growing interest on the ecological consequences of individual's differences in behaviour, especially those linked to affect-driven decision-making, underscores the significance of investigating the emotional aspect of animals' life (Laskowski et al., 2022).

In psychology, speech reports are usually employed as a benchmark for inferring human's emotional experiences and measuring their subjective or "conscious" quality. Due to the absence of such indicators in animals, biological research primarily investigates animal emotions by focusing on their function instead (Paul et al., 2005). That is, on the mechanisms by which emotions assist organisms in coordinating different resources to efficiently navigate environmental challenges. For instance, when faced with a threat, fear is considered to prompt organisms to fight or flee, modulate their heart rate, and sharpen their attention. Thus, despite the absence of evidence of animals' conscious experience of affective states, the investigation of their affective states' proceeds by identifying their putative behavioural, physiological, and cognitive components, alongside their eliciting conditions.

Within this endeavour, researchers typically delineate the contrast between positively and negatively valenced states in terms of opposite motivational tendencies, where positive states prompt approach and negative states elicit aversion towards the object of the affective state (e.g., Lang, 1995). This assumption has been particularly prominent within the Judgment Bias Test (JBT), which explores the influence of affective states on decision-making by measuring animals' responses to ambiguous stimuli (Harding et al., 2004; Mendl et al., 2010). In a standard JBT, animals initially learn to respond differently to two distinct cues that signal a positive or a negative outcome (e.g., food rewards or punishments, respectively). Subsequently, when confronted with intermediate, ambiguous cues, their behavioural responses—namely, approaching or avoiding such cues—serve as indicators of the organism's relative degree of bias to judge them as expecting rewards (i.e., "optimism") or punishments (i.e., "pessimism").

This framework has facilitated cross-species comparison of affect-related decision-making, spanning mammals, fish, and insects, thereby offering valuable insights into ultimate question regarding the evolutionary significance of affective states (Lagisz et al., 2020). However, it bears certain limitations. Outside the laboratory, event's outcomes often defy neat categorization as purely rewarding or punishing. Confronted with such events, foraging organisms may judge potential energy gains more valuable than safety, leading them to seek rewards (i.e., display "risk-prone" behaviour) or, conversely, consider safety more valuable than energy gains and consequently attempt to avoid them (i.e., display "risk-averse" behaviour). According to the framework outlined above, risk-prone behaviour would be thus associated with a positive state, reflecting an overall evaluation of the situation as rewarding. However, risk-prone behaviour has also been observed to correlate with anxiety and aggressiveness (Sih et al., 2004), states that would be inaccurate to describe as positive**.**

This case, along with extensive evidence indicating that "liking" and "wanting" a stimulus do not always converge (to be reviewed in Section 2.3), calls for a more nuanced framework to investigate affect-related decision-making. In pursuit of this goal, this paper aims at defending a new operational definition of affective states that introduces a conative dimension: "dominance". The basic idea is that, whereas the activation of valence is influenced by how rewarding or punishing an environment is, the activation of dominance involves how capable individuals perceives themselves to obtain such rewards or overcome such punishments. While early dimensional models of affect featured such a conative dimension (Osgood et al., 1957; Mehrabian & Russell, 1974), these were later considered peripheral to "core affect", namely, valence and arousal (Russell & Barrett, 1998; Barrett & Russell, 1999). Hence, this paper proposes a definition of dominance as a measurement of the organism's subjective experience of behavioural self-control vis-à-vis environmental challenges and addresses the criticisms against its inclusion in the definition of core affect (Section 3).

Drawing inspiration from Mendl et al. (2010), this paper develops a behavioural operationalization of the "Valence-Arousal-Dominance" framework (Section 4). The framework is explored for its potential applications in two domains. Firstly, I argue that the interplay between valence and dominance can offer insights into state-of-the-art experimental research on animal risk-taking behaviour, drawing an example from Bračić et al. (in review) (Section 5). Secondly, I explore how dominance might elucidate not only the influence of emotions on animals' survival but also on their thriving. Inspired from Hintze & Yee (2023), I link dominance to the study of "flow" in animals, namely, a state of absorption that requires the equilibrium between individual capabilities and environmental challenges (Section 6). Through these applications, this model aims to bring experimental paradigms of animal affect-related behaviour closer to ecologically relevant scenarios.

2 Background: the study of animal affect-related decision-making

2.1 Varieties and models of affect

Affective states come in various types. Emotions like joy or anger are standardly considered states directed towards particular stimuli provided by their cognitive bases (e.g., perception or memory) (Kenny, 1963). Moods such as grumpiness or elation, in contrast, are considered relatively enduring states that lack a specific object, and that trigger emotions of the same affective colour (and vice-versa) (Frijda, 1994a). Being grumpy, for instance, may incite an organism to feel angry, and feeling angry may induce a state of grumpiness. Alternative taxonomies of affective phenomena also include personality or "character" traits such as boldness, aggressiveness, or optimism. Like moods, traits are said to motivate particular reactions: if someone is aggressive, for instance, they will display a greater than typical tendency to feel, say, anger or anxiety. However, in contrast to moods, character traits lack a subjective quality, except derivatively through the affective states in which they find expression (Deonna & Teroni, 2012).

When investigating these phenomena, affective states are conceptualized through either discrete or dimensional models. Discrete models conceptualize emotions, such as anger or fear, as natural kinds with specific behavioural, physiological, and cognitive 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 FEAR, 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 responses (e.g., different patterns of autonomic activation) can be associated with a single emotion-type and that, conversely, different emotion-types (e.g., anger and joy) can be associated with similar physiological responses, raising scepticism about whether different types of emotions share intrinsic properties (Barrett, 2017).

Alternatively, dimensional models view affective states as composed by more fundamental building blocks. One prominent model in this category is the "Circumplex Model" (Russell, 1980). In contrast to the discrete model, which posits that independent neuronal systems subserve each emotion-type, the circumplex model proposes that all affective states arise from two neurophysiological systems. One system is related to valence—the "hedonic" quality of the state, which can range from negative to positive—while the other to arousal—the degree of physiological activation, which can range from low to high. A specific affective state can be thus located along two orthogonal dimensions, with the X-axis representing the degree of valence and the Y-axis representing the degree of arousal. For instance, in this framework "Happy" and "Content" would arise from the same two neurophysiological systems but differ in their degree of arousal (see figure 1). While the analysis of animal's discrete states has traditionally received more attention—see, for instance, De Wall & Preston (2017) on animal empathy—, the dimensional perspective has gained prominence within the field of behavioural biology, as we will explore in the next section.

2.2 Circumplexity and the Judgment Bias Test

Research in human psychology suggests that alterations in information processing serve as a reliable indicators of individuals' emotional states (e.g., MacLeod & Byrne, 1996). People undergoing negative states, such as depression or anxiety, tend to make more negative judgments about ambiguous stimuli relative to their counterparts in more happier states. Recently, these findings have sparked interest on whether such affect-induced biases exist in animals as well, in particular through the judgment bias paradigm (Harding et al., 2004; Mendl et al., 2010). In this section, I describe how the circumplex model is conceptualized and applied within this paradigm.

Mendl et al. (2010) proposes to associate the transition from non-arousing, negative states to highly arousing, positive states with the activation of the "reward acquisition" system (RAS). Conversely, the shift from non-arousing, positive states, to highly arousing negative states is proposed to involve the "punishment-avoidance" system (PAS) (see also Mendl & Paul, 2020). These "biobehavioural mechanisms" are assumed to 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.) (Watson et al., 1999). Figure 1 illustrates the resulting functional interpretation of the structure of core affect:

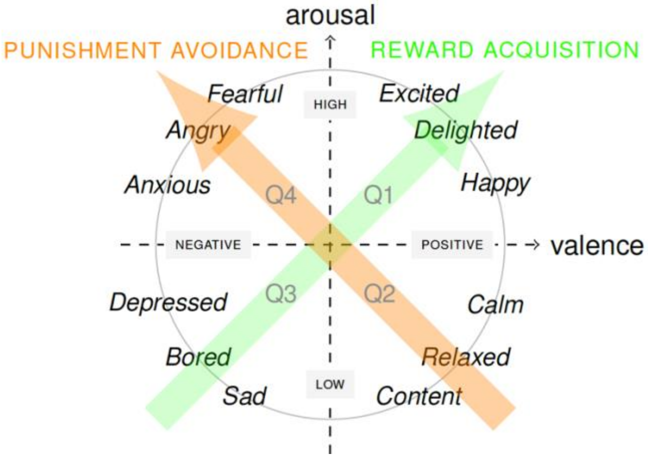

Fig. 1 Functional operationalization of the Circumplex Model, adapted from Mendl et al. (2010). The X-axis represents the valence dimension and the Y-axis the arousal dimension. Words in italics indicate the location of specific affective states, including emotions ("Fearful") and moods ("Anxious"). Arrows indicate the hypothetical link between the reward acquisition system and the Q3-Q1 axis (green), and the punishment avoidance system and the Q2-Q4 axis (red) proposed by Mendl et al. (2010)

Grounded on evidence that judgment bias in humans may be indicative of their positive or negative states, the framework proceeds to map the Q1-Q4 states with types of decision-making. Q1 states are postulated to trigger decisions appropriate to high reward-opportunity environments, and thus to reflect individuals' high expectation of positive events, and Q2 moods to trigger decisions reflecting low expectation of negative events (i.e., "optimistic biases"). Conversely, Q3 moods trigger decisions associated with low expectation of positive events and Q4 moods those associated with high expectation of negative events (i.e., "pessimistic biases").

Bases on this framework, the Judgment Bias Test typically comprises the following three phases (Nematipour et al., 2022):

A. During the training phase, animals are presented with "positive" cues, which result in a reward, and "negative" cues, which result in a punishment (e.g., white noise). Through repeated trial and error, animals learn to respond positively by approaching the reward-associated stimuli and negatively by avoiding the punishment-associated stimuli. That is, by activating the RAS and PAS.
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' expectations of positive or negative outcomes, operationalized as "optimistic" or "pessimistic" biases, and thus of their location in the valence-arousal space (Q1-Q4).
C. In the priming phase, a subset of animals undergoes a treatment intended to alter their affective state (their mood) 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.

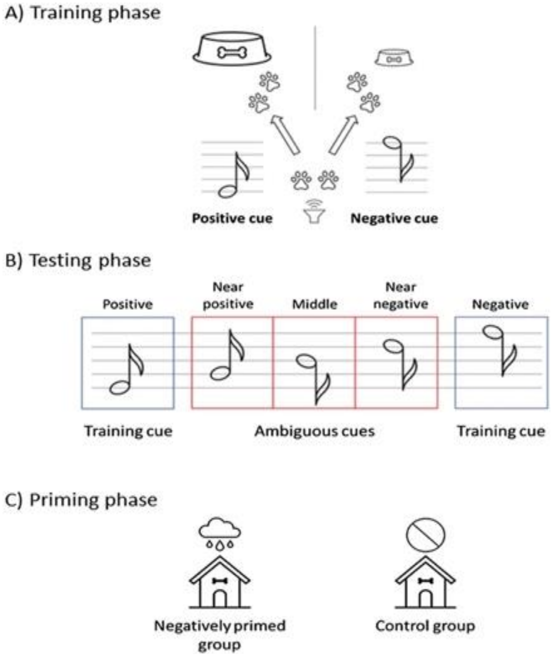

Fig. 2 Example of the JBT design in Nematipour et al. (2022), representing A) the training phase, where animals are presented with low and high-pitched tones; B) the testing phase, where animals are also presented with pitches intermediate to the training tones; and C) the priming phase, where a subgroup of the animals is exposed to unpredictable housing to induce a negative state before testing

The outcomes of a JBT with negative priming has found significant differences between treatment and control groups across species. In general, animals undergoing a treatment hypothesized to trigger negative states exhibit a pessimistic bias by responding more often in the negative way to the ambiguous cues compared to those of the control group (Lagisz et al., 2020). This outcome not only demonstrates the paradigm's ability to detect changes in affective states but also provides evidence that the applied priming manipulation has a lasting impact on the animals' positive or negative states. Importantly, it also constitutes an illustration of the valence-arousal model's ability to generate testable hypotheses concerning animals' emotional experiences.

2.3 Issues in bi-dimensional affect: distinguishing "liking" from "wanting"

While this model provides a useful foundation for empirically investigating affect's influence on animals' cognition, it encounters serious limitations. As observed, the model aligns affective states with systems governing approach and avoidance behaviours, positioned at a 45º angle to the core affect axes (see figure 1). Yet, this assumption is not straightforwardly true. In humans, addictive disorders involve seeking stimuli even in the absence of pleasure (Berridge et al., 2009). In animals, activities such as "predator inspection" involve approaching stimuli that are potentially dangerous (Blaszczyk, 2017). Using Berridge et al.'s, (2009) terminology, "wanting" and "liking" a stimulus may be sometimes dissociated from each other.

Instances of this nature not only represent a deviation from the norm but are also observable in some animals' daily lives. Within the JBT, behavioural responses indicate organism's attitudes towards stimuli that may be either rewarding or punishing, but not both. However, during foraging under predation risk, animals often find themselves in situations that encompass both rewarding and punishing aspects, such as challenging-to-access food resources. In these situations, organisms may prioritize energy gains over safety, displaying risk-prone behaviours, or safety over energy gains, thus displaying risk-averse behaviours. Risk-prone behaviours entail seeking and thus approaching a stimulus. Hence, using the framework outlined in section 2.2, these behaviours might be construed as a proxy for organisms' positively valenced states. However, this interpretation would be inaccurate. Risk-prone dispositions also appear to correlate with anxiety and aggressiveness (Sih et al., 2004), suggesting that pleasure and motivational tendencies do not typically align.

A standard proposal for characterizing risk-related attitudes posits that organisms rank their needs and motivations using valence as a "common" currency (Cabanac, 1992). When faced with conflicting motivations, organisms would aim at selecting the option that maximizes pleasure. In scenarios where accessing food involves facing threats, for instance, animals would assess potential energy gains against the risk of predation based on their current energy balance, ultimately deciding for an "overall" evaluative response—e.g., approaching the stimulus despite the threat of predation due to the organism's hunger. Thus, in this account, we wouldn't need to abandon the assumption that positive [negative] polarity aligns with approaching [avoiding] behaviours, as positive states would trigger approach only in cases where it is, overall, stronger than negative states.

Recent research has provided compelling experimental evidence of this "expected utility" approach to animal decision-making (e.g., Verdolin 2006). However, many studies have also failed to demonstrate optimal foraging behaviour under predator risk. The likelihood of a higher number of negative results exists, mainly due to general publication bias against negative findings (Dammhahn & Almeling, 2012). Certain organisms exhibit risk-prone or risk-averse behaviour regardless of their energy budget. Consequently, risk-taking cannot be solely attributed to optimal trade-off calculations regarding the valence of different stimuli. The presence of sub-optimal animal risk-taking behaviour underscores the necessity of exploring additional factors that may influence animals' decision-making.

A prominent approach for investigating sub-optimal behaviour involves assessing an animal's personality. In the biological context, personality is defined as the interindividual consistent variation in behavioural traits (Sih et al., 2004; Réale et al., 2007). For instance, stable individual differences in risk-taking behaviour are termed "boldness", hypothesized to be an important source of variation constraining decision-making. However, although it is unclear whether personality traits can be considered "affective", organisms' personality has been observed to interact with their affective states, thereby constraining their behavioural flexibility (see section 2.1). In line with this premise, there is evidence that both organism's personality and mood influence certain species' cognitive biases (Asher et al., 2016). Therefore, it is important to study risk-taking behaviour not only in relation to personality traits, but also in relation to the emotions these traits may trigger. Achieving this requires a novel framework of affect that clearly distinguishes valence from motivation. In what follows, I argue that adding a conative dimension, beyond valence and arousal, provides the required nuance.

3 Introducing the Dominance dimension

3.1 Three theoretical proposals

The divergence between liking and wanting in decision-making expounded in the last section calls for a more nuanced theory of the structure of emotions. In this section, I briefly contrast three strategies to enhance dimensional models within the study of human affect. First, to distinguish qualitatively different states, constructivist theories incorporate a categorization process between the experience of affect and its outcomes (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).

Second, appraisal theories of emotions distinguish between emotional states by interposing a stimulus evaluation process between what is perceived and the experience of affect (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, despite the potential of exploring the application of the appraisal view in animal behaviour research, the appraisal theory primarily focuses on emotions. Yet, we require a comprehensive framework that can encompass moods and, if possible, attitudes such as optimism as well.

Third, it is worth considering that "core affect" is not limited to valence and arousal (Fontaine et al., 2007). Early dimensional models of affect often included such a third, "conative" dimension. These models were first introduced within the so-called "Semantic Differential Technique" framework, which aimed at measuring the affective meaning of emotion-related words and other stimuli using bi-polar scales (Osgood et al., 1957). Mehrabian & Russel (1974), for instance, proposed the 'Pleasure-Arousal-Dominance' (PAD) model to study the degree to which individuals perceived a stimulus as pleasant (positive-negative), arousing (high-low) and dominant (dominant-submissive). The PAD model soon extended its scope of application, encompassing the development of metrics for emotions (Russel & Mehrabian, 1977) and personality traits (Mehrabian, 1996). As an illustration, consider Mehrabian (1996)'s model, depicted in figure 3. Although designed to distinguish between personality traits, states such as "Relaxed" or "Anxious" can also be described as moods:

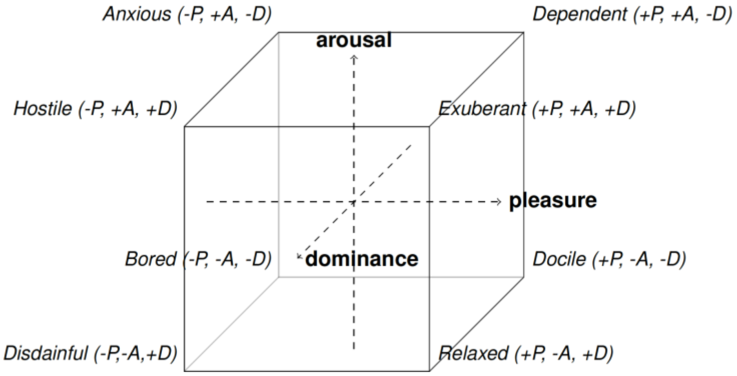

Fig. 3 PAD model's space of personality traits adapted from Mehrabian (1996)

The addition of a conative dimension has the potential to provide a more nuanced picture of affect that allow us investigate decision-making in risk-taking contexts. However, various obstacles need to be surmounted before applying such model. First, while dominance was described through different expressions such as "controlling", "influential" or "autonomous" (Mehrabian & Russel, 1974; Russel & Mehrabian, 1977), a clear definition of it was missing (Bakker et al., 2014). Second, within SDT studies, stimuli ratings along dominance were not always independent of the other two dimensions (Russell & Mehrabian, 1977). As a result, current dimensional models redefine dominance as denoting assessments of the antecedents and consequences of the affective experience, thereby acknowledging it as a cognitive process, peripheral to core affect (Russell 1978; Russell & Barrett, 1998). I will dedicate the following subsections to address these two issues.

3.2 Dominance as (self-)control

The label "dominance" does not only have many usages in ordinary language, but also has been used in different ways within dimensional models of affect (Bakker et al., 2014). Hence, before discussing whether dominance may or not pertain to core affect, we need to put the concept of dominance on a better theoretical ground. The psychological literature on (self-)control, I think, offers a 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 (1989) examined the interplay between primary/secondary control and positive/negative evaluations. As a result, he proposed a four-factor model of perceived control, 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 animals' affect-related decision-making, the focus will be directed towards primary control. Therefore, I define dominance as a parameter related to an individual's inherent drive or inclination as determined by their self-assessed behavioural capacity to obtain positive events and avoid negative ones. Thus, whereas valence, the hedonic quality of an affective experience, is influenced by individuals' attitudes towards the likelihood of a stimulus being positive or negative, dominance is based on an individual's assessments of their own capability to secure the former and evade the latter. This latter 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 consider 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).[1]

3.3 Rethinking core affect

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[1] Within the literature on agency, the subjective character of decision-making is termed "sense of control". Pacherie (2007) delineates its three distinct components: i) "rational control", which involves ensuring the steps to attain a goal; ii) "situational control", which considers agents' characteristics, the target of action and the surrounding context; iii) finally, "motor control", which specifies the detailed parameters of the selected motor program. The definition of dominance I propose would therefore align with situational control, albeit positioned here as subjective sensation on par with valence and arousal. Thanks to an anonymous reviewer for highlighting the necessity to explore the relation between the feeling of dominance and agency.

Having provided a definition of dominance, I turn to the empirical, conceptual, and methodological issues regarding its inclusion in the definition of core affect. First, as observed above, individuals struggled to rate stimuli (e.g., isolated words) along a dominance scale (Russell & Mehrabian, 1977). However, more recent studies show that individuals do indeed factor on the dominance dimension when assessing other type of stimuli such as facial expressions (Oosterhof & Todorov, 2008) or social interactions (Moors & De Houwer, 2005). This discrepancy in the relevance of dominance may be attributed to the type of stimuli used within these studies (e.g., isolated stimuli like words vs. social interactions). Hence, relying on verbal reports may be insufficient to settle theoretical debates about the dimensions of affect (Harmon-Jones et al., 2017).

Second, the rationale behind the location of dominance as a cognitive process and thus peripheral to core affect bears some conceptual shortcomings, as researchers nowadays acknowledge that the cognitive-non-cognitive demarcation is not as clear-cut as standardly considered. In philosophy, emotions are described not only as having cognitive bases (i.e., are anchored on perception or memory) but also possess representational properties (i.e., qualify stimuli as being a certain way and can be subject to rational justification) (De Sousa, 2003). In some versions of the appraisal theory in psychology (introduced in section 3.1), cognitive assessments of the environment are not considered causes of affective states but part of the experience of affect itself. Lastly, within evolutionary psychology, it is standardly considered that emotions evolved across species to coordinate adaptive responses through behavioural control (e.g., Frijda, 1994b). If so, it becomes surprising that dominance, which precisely highlights individuals' internal sense of behavioural influence over their surroundings, is considered peripheral to affect.

Finally, 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). This is particularly clear on cases where, by so doing, researchers can generate tractable hypotheses about emotions' effects. Within the JBT paradigm, introduced in section 2.2, models of affect 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. Nevertheless, instead of assuming that valence and arousal offer a predefined, optimal approach to characterize the whole spectrum of affective states, affect can be 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). Therefore, to overcome the limitations of valence and arousal in accounting for cases where wanting and liking do not align (see section 2.3), there arise a necessity to refine our definition of affect's structure. I propose a way to achieve this in the next section.

4 The VAD model in animal behaviour research

To develop of a more ecologically oriented model of animal affect, let's begin by considering optimal foraging theory. To model how animals make decisions, this theory identifies both the "currency" and "constraints" that may exert influence (Pyke, 1984). While currency refers to the unit optimized by the animal, such as energy intake, constraints to those factors that limit foraging efficiency, such as predator's presence. In simpler terms, currency is the measure on which foragers assess costs and benefits, while constraints relate to perceived behavioural limits. Analogously, I propose that a model of animal affective states needs to differentiate between its valence—representing the weight attributed by the organism to fitness-enhancing or fitness-detrimental stimuli—and dominance aspects— reflecting how prepared the organisms perceive themselves to obtain the former and avoid the latter. Yet, how do these two dimensions, together with arousal, interrelate to neuronal systems, moods, and biases raises pertinent question, each of which I will address in what follows.

4.1 Neuronal systems and basic emotions

As both currency and constraints need to be considered in elucidating foraging behaviour, I propose that the Reward Acquisition System (RAS) activates not only to guide organisms in obtaining positive states but also those characterized by high dominance (cf. the green arrow in figure 4.1). Conversely, the Punishment Avoidance System (PAS) operates not only to avoid negative states but also those marked by low dominance (cf. the orange arrow in figure 4.1). These systems explain situations where liking and wanting do overlap. Nevertheless, owing to the wide spectrum of scenarios encountered by foraging animals—ranging from highly rewarding yet dangerous stimuli to poorly rewarding yet safe surroundings—individual organisms are assumed to perform optimal trade-offs to determine an overall behavioural response. However, as observed in section 2.3, evidence showcasing sub-optimal decision-making suggest the involvement of additional factors in this process.

Due to the relevance of efficiently navigating these complex scenarios, it is standardly assumed that some species not only engage in optimal calculations but have also evolved more specific neuronal systems finely tuned for this purpose. Panksepp's (1998), for instance, postulated the existence of four innate emotional circuits termed SEEKING, FEAR, RAGE, and PANIC. While SEEKING prompts individuals to forage for rewards while coping with punishing aspects of the world (Wright & Panksepp, 2012), the FEAR system drives individuals to ensure survival. Using the VAD model, I posit that these two future-oriented systems elucidate situations where liking and wanting do not overlap. While SEEKING serves to maximize valence despite environmental challenges (cf. the blue arrow in figure 4.2), FEAR to secure safe, albeit less rewarding, outcomes (cf. the yellow arrow in figure 4.2).

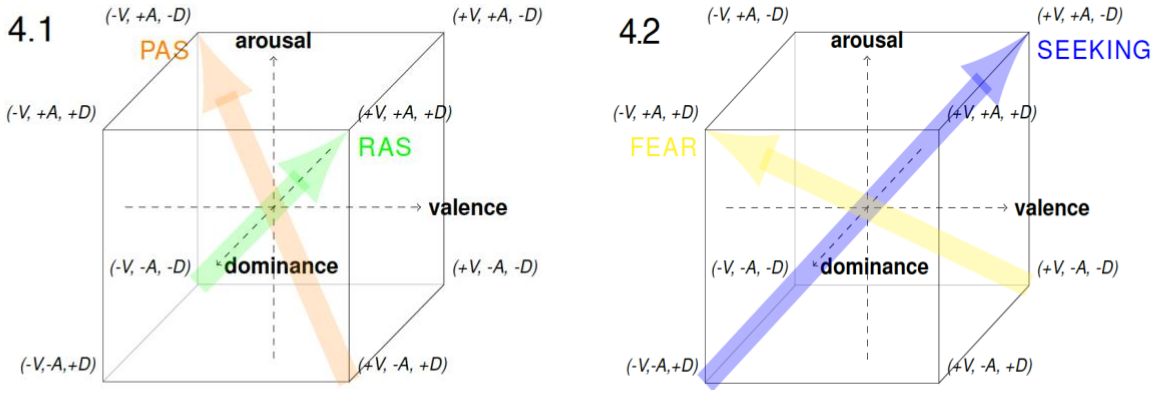

Fig. 4 VAD's model space. In the figure 4.1, the arrows indicate Mendl et al.'s (2010) putative biobehavioural systems, including the Reward Acquisition System (depicted in green) and the Punishment Avoidance System (depicted in orange). In contrast, Panksepp's (1998) emotional programs SEEKING (depicted in blue) and FEAR (depicted in blue) are featured in figure 4.2

Before moving further, two aspects of the model warrant attention. The first regards the grounds for incorporating discrete affective programs such as SEEKING and FEAR into a dimensional framework. Despite the conventional view of discrete and dimensional models of affect as rivals, many authors have also emphasized that there is psychological, neural, and behavioural evidence for both (e.g., Panksepp, 2007; Harmon-Jones et al. 2017; Mendl et al., 2010). Hence, I suggest the co-existence of basic emotion programs and core affective dimensions in the brain, where they serve complementary functions. In this hybrid perspective, affective dimensions provide a functional scaffold for the integration of basic affective programs such as SEEKING, FEAR, and potentially others specialized neuronal circuits, elucidating their interplay and adaptive significance.

Secondly, it is important to note that SEEKING represents an "expansion" of RAS. According to Wright & Panksepp (2012), while reward circuits only involve hedonic pleasure, SEEKING relates to foraging, action-oriented drives, appearing more like euphoria than pleasure. Additionally, drawing inspiration from Bach and Dayan (2017), we can appeal to instrumental reinforcement learning to elucidate this difference. In this framework, decision-making can be either "model-free" (when organisms select actions only based on their value) or "model-based" (when organisms additionally weight the anticipated outcome of those actions). Thus, while PAS and RAS only focus on stimuli value (namely, on how rewarding or punishing the stimulus is), and thus are model-free, pre-programmed responses like SEEKING and FEAR also focus on anticipated outcomes (namely, on how those rewards are punishments are to be obtained or avoided), and thus can be considered model-based.

4.2 Moods and decision-making

As proposed by Mendl et al. (2010), moods are relatively enduring, objectless states that provide information about the prevailing environmental conditions the organism experiences. For instance, a depressed individual may be inclined to perceive their environment as anticipating adverse outcomes (e.g., MacLeod & Byrne, 1996). In other terms, a depressed mood triggers decisions suited for dealing with those events, that is, guides or "bias" cognitive responses. These moods may result from habitual exposure to punitive environments or from innate behavioural dispositions.

Before specifying moods' effects in a three-dimensional space, an extensional definition of them needs to be provided. To characterize moods, I label each octant O1-O8 of the VAD space using Mehrabian's (1996) model of personality traits (as depicted in figure 3). However, as observed in section 3.1, states such as "Relaxed" or "Anxious" can be considered more appropriately belonging to the realm of moods—namely, occurrent object-less states. Personality traits will be discussed in subsection 4.3.

Now, let's outline moods' specific effects. In Mendl et al. (2010), different moods are correlated to distinct attitudes. For instance, Q3 moods are associated with low expectation of positive events, while Q4 moods with a high expectation of negative events (as illustrated in figure 1). Hence, alterations in arousal invert the expectation's direction, but not the state's hedonic quality. When extrapolating this perspective into the VAD space, moods function analogously. That is, changes in arousal's alter individual's expectations, but not the states' hedonic or dominance qualities. Hence, we can classify moods into the following four groups:

- The first class comprises the O1 mood ("Exuberant"; +V, +A, +D), associated with decision-making reflecting high expectation of safe and rewarding events, and the O2 mood ("Relaxed"; +V, –A, +D), aligning with decisions indicating low expectations of non-rewarding, risky events.
- The second class includes the O5 mood ("Dependent"; +V, +A, –D), associated with decisions reflecting high expectation of rewarding yet risky events, and the O6 mood ("Docile"; +V, –A, –D), indicating decisions reflecting low expectation of non-rewarding yet safe events.
- The third class consists of the O4 mood ("Hostile"; –V, +A, +D), correlated with decisions reflecting high expectations of non-rewarding but safe events, and the O3 mood ("Disdainful"; –V, –A, +D), which denotes decisions reflecting low expectations of rewarding but risky events.

- Lastly, the fourth class includes the O8 (“Anxious”; –V, +A, –D), connected with decisions reflecting high expectation of non-rewarding, risky events, and the O7 (“Bored”; –V, –A, –D), which corresponds to decisions reflecting the low expectation of rewarding but safe events.

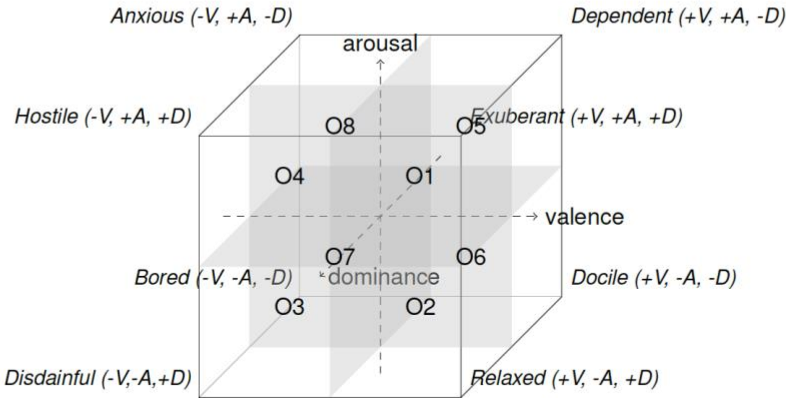

Fig. 5 Regions of the VAD’s model space, where eight stipulated moods are hypothesised to provide decision-making adequate to engage with different types of environments

Before proceeding, it is noteworthy to observe the differences between Mendl et al.’s (2010) model and our framework. In the former, the mood marked by Q4 is functionally associated with the activation of the PAS. In contrast, in the VAD model, the activation of the PAS is attributed to the O8 mood (“Anxious”), while the recently incorporated FEAR circuit is attributed to the O4 mood (“Hostile”). This proposition may seem inadequate, given that the FEAR circuit can ostensibly encompass both anxiety and hostility. However, despite the potential for refinement in the identification of these moods, it is important to acknowledge their pragmatic role as descriptors of regions in the three-dimensional space, which may or not completely encapsulate folk mood notions.

Indeed, the merit of this assumption regarding moods lies in its potential to opens new venues for elaborating cross-species comparisons of affective-related behaviour. In the JBT, organisms are primed to be in negatively valenced states before testing to measure alterations on their decision-making (as described in section 2.2). With the VAC model, we could additionally formulate hypotheses about how the experience of different types of negative priming may influence behaviour. This will be discussed in sections 5 and 6. Prior to that, however, we need to explain what such bias are in the VAD model.

4.3 Cognitive biases

In Mendl et al. (2010), both Q1 and Q2 moods are linked to positive expectations, while Q3 and Q4 states are linked with negative expectations. The former moods are termed “optimist” and the latter “pessimist” biases in decision-making. In our model, in contrast, individuals that show enhanced expectation of (+V, +D) events—i.e., those prone to an “Exuberant” or “Relaxed” mood—are optimist, and those that show enhanced expectations of (–V, –D) events—i.e., those inclined towards an “Anxious” or “Bored” mood—are classified as pessimist (see figure 6). Following Mendl et al. (2010), I assume that these states hold particular relevance in situations where incoming sensory information is ambiguous and yet individuals’ survival depends on taking an optimal decision.

However, as discussed earlier, individual behavioural responses may also exhibit variation with respect to their assessments of reward and safety trade-offs, namely, in indicating whether the organism considers that potential benefits outweigh risks or vice versa. I refer to these different attitudes as risk-prone and risk-averse attitudes. Whereas Mendl et al. (2010)'s model does not encompass these attitudes, in the VAD model we state that individuals that tend to favour (+V, –D) events (i.e., those that tend to be in a "Dependent" or "Docile" mood) are considered risk-prone, and conversely, those that tend to favour (–V, +D) events (i.e., those that tend to be in a "Hostile" or "Disdainful" mood) are considered risk-averse. In section 5, I contend that these states are particularly relevant in situations where incoming sensory information is ambivalent and yet individual's survival relies on taking an optimal decision.

Before moving on, two aspects should be analysed. The first is that it is worth stressing that the optimism/pessimism and risk-prone/risk-averse continua are posited to be independent within this model. As illustrated in figure 6, examining the VD plane of the VAD model reveals that these attitudes form two continua at 45 degrees such dimensions. However, this assumption needs to be empirically investigated. Specifically, it may emerge that organisms which are more optimist (with respect to ambiguous stimuli) also tend to display a higher inclination towards risk-prone behaviour (with respect to ambivalent stimuli). In section 5, empirical support for this assumption will be discussed.

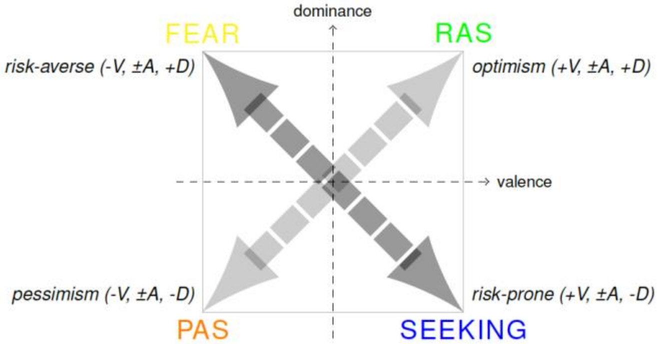

Fig. 6 This figure illustrates the V-D plane of the VAD's model space, where the four stipulated attitudes, namely the optimist/pessimist and risk-prone/risk-averse attitudes, are depicted as constituting independent, orthogonal continua

The second aspect for consideration pertains to the relationship between these attitudes and personality traits, namely, stable behavioural responses. Here, I posit that optimist/pessimist or risk-prone/risk-averse behaviours can indicate a particular personality but do not constitute sufficient evidence thereof. In the biological domain, personality traits are assumed to hinge not solely on a singular type of observed behaviour, but on various of them, which should be displayed by the individual across a relatively wide timeframe (Kaiser & Müller, 2021). For instance, while observing risk-prone attitudes may serve as indicator of a boldness personality, its measurement should be complemented by the examination of other boldness traits, such as the motivation to explore novel objects within an experimental setting (Blaszczyk, 2017).

5. Applications (I): optimism vs. risk-taking

As in section 2.2, the JBT measures behavioural responses to experimental conditions possessing the potential for either reward or punishment, assumed to elicit positive or negative states, respectively. However, ecologically relevant situations present stimuli that intertwine both features. To understand animals' decision-making with respect to this kind of situations, I refer to the work of Bračić et al. (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 an 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 (e.g., illumination) but yielding a substantial reward and b) "the safe chamber", containing clean bedding yet yielding a small reward (see figure 7). The mice's decision-making rates are quantified as "choice score".[2]

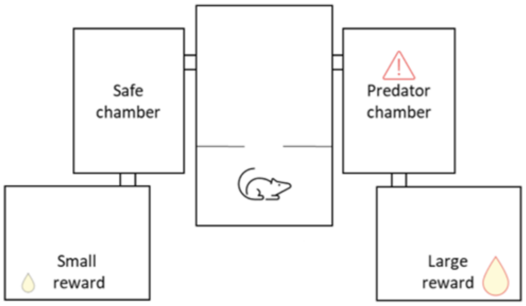

Fig. 7 Environment Choice Test (Bračić et al., under review). The test apparatus consists of five interconnected chambers. On each side, there are cue chambers where predator cues ("predator chamber") or clean bedding ("safe chamber") are introduced. During the test, mice need to traverse one of these 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 states. 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 triggering (+V, –D) and (+V, –D) states. Consequently, as per the definition of attitudes outlined in Section 4.3, consistent reactions to these cues can be construed as reflecting individuals' attitudes: mice are risk-taking when favouring the predator chamber and risk-averse when evincing a predilection for the safe chamber. Aggregating these decisions can thus be quantified as a "risk score".

Moreover, as we saw in section 4.3, the VAD model posits that optimist/pessimist and risk-prone/risk-averse attitudes engage distinct behavioural systems. Specifically, the RAS/PAS and the SEEKING/FEAR systems, respectively (cf. figure 6). Thus, the model predicts absence of correlation between optimist and boldness moods. Bračić et al.'s finding that optimism and choice (i.e., risk) scores do not correlate can be interpreted as substantiating such prediction, that is, as confirming the

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[2] 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.

VAD model's assumption that multiple attitudes may co-exist within the same individual (thus creating "behavioural syndromes"; see Sih et al., 2004).

The VAD model also bears the potential to assist in further supporting research that involves probing the influence of individual's affective state on behavioural decision-making. In the JBT, it is confirmed that individuals' states of depression or anxiety influence their degree of optimism. Using the VAD, we could also investigate whether negative states also influence their propensity for risk-taking. Inspired on the three-step study in the JBT, in a new mechanistic study, one can, for example, induce stressors or other treatments on a randomly selected sub-group of individuals, and then track whether and to what extent treatments make them risk-prone or risk-averse following Bračić et al.'s (under review) paradigm. Evidence showing that animals' health (Heithaus et al., 2007), nutrition (reviewed in Moran et al., 2020), and stress (Sih, 2011) affect their degree risk-prone behaviour substantiate such hypothesis (however, see Niemelä & Dingemanse, 2018).

However, we can go beyond with respect to valence-related priming. To wit, the VAD model provides a platform to examine new mood-modulated decision-making through manipulative experiments. In a different type of manipulative experiments, we could employ negative primings that variate in their degree of control/dominance. For example, we could use similarly rewarding locations which present various degrees of safe or risk for the individual organism. More particularly, equally poor food rewards could be placed in locations with more or less predator cues before testing. Subsequently, we would see how subgroups primed with a rewarding but non-dominant location vs. dominant location become more or less optimist or risk-prone.

The advantage of conducting this type of behavioural study against the background of the VAD model extends to its capacity to generate translatable hypotheses regarding affect-related decision-making. To wit, even though the optimist-pessimist continuum has been functionally defined (using affective dimensions) as individual's expectations of positive or negative outcomes, the risk-taking continuum typically escaped such mapping. Thus, by unifying them under a multidimensional framework of affect, we can achieve a more complete picture of the structure of animal affect (for insights into the unifying role of explanations, see Kitcher, 1981). In the next section, I discuss how dominance can also help us to look at living conditions beyond the presence of rewards, punishments, or combinations thereof.

6. Applications (II): hedonic vs. cognitive enrichments

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, e.g., Fredrickson, 2001).[3] 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 & Yee, 2023, 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 (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 (see, however, Clark, 2023, for a study of intrinsic motivation in

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[3] Thanks to […] for drawing my attention to this aspect.

primates). 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 & Yee, 2023; Clark, 2023). 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. Thus, following the VAD model outlined in Section 4, I decompose affective states in their valence aspects, understood as a subjective aspect mainly modulated by the acquisition of rewards such as food or shelter, and dominance aspects, understood as a subjective aspect modulated by the potential success in overcoming environmental challenges. Importantly, for both affective dimensions, 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 follows:

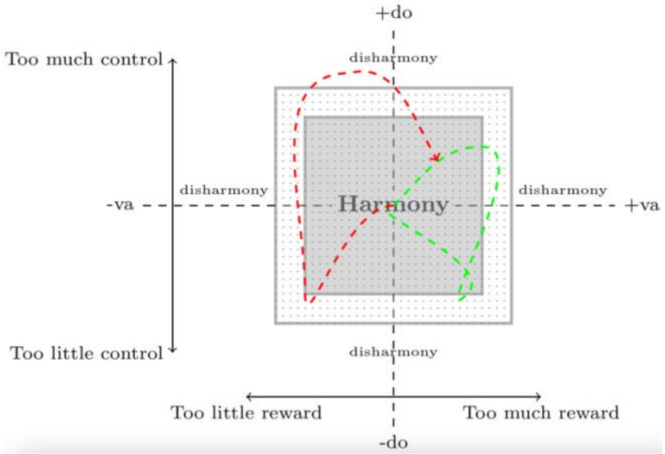

Fig. 8 Harmony space. The levels of reward and control serve as indicators of harmony and disharmony in an animal’s perceived environment. The green and red dashed lines indicate hypothetical scenarios of an organism’s affective states fluctuating over time. The green line represents cycles characterized 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 8. However, as depicted by the red dashed line, this cycle could be interrupted by another cycle where losing access to the shared reward may generate anxiety (–V, –D) or hostility (–V, –D). Insofar as green and red cycles do not 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). That is, we could induce animals to experience varying degrees of equilibrium and disequilibrium in the interplay between their skills and environmental challenges. 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. To ascertain whether flow has been effectively induced, researchers can assess an animal’s resistance to increasingly attractive external distractions, considering the species’ ecological niche and the typical challenges it confronts.

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. Hence, I introduce the concept of flow in the context of animal welfare to highlight the potential of animal’s subjective sensation of dominance/control to unlock moments of optimal engagement and fulfilment (for a recent discussion of this potential from the point of view of animal agency rather than affective states, see Littlewood et al., 2023). However, I 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.

8. Conclusion

Research across species underscores that animals can be sophisticated evaluators of the quality of their environment, for example, by weighing multiple factors to make 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 risk-prone/risk-averse 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.

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