Affective styles and emotional lateralization: A promising framework for animal welfare research

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ABSTRACT

The growing recognition of animals as individuals has broader implications for farm animal welfare research. Even under highly standardized on-farm conditions, farm animals show heterogeneous but individually consistent behavioural patterns towards various stimuli, based on how they appraise these stimuli. As a result, animal welfare is likely to be highly individual as well, and studying the proximate mechanisms underlying distinct individual behaviour patterns and appraisal will improve animal welfare research. We propose to extend the framework of affective styles to bridge the gap between existing research fields on animal personality and affective states. Affective styles refer to consistent individual differences in emotional reactivity and regulation and can be predicted by baseline cerebral lateralization. Likewise, animals with consistent left or right motor biases—a proxy measure of individual patterns in cerebral lateralization—have been shown to differ in their personality, emotional reactivity, motivational tendencies or coping styles. In this paper, we present the current knowledge of the links between laterality and stable individual traits in behaviour and affect in light of hypotheses on emotional lateralization. Within our suggested framework, we make recommendations on how to investigate affective styles in non-human animals and give practical examples. This approach has the potential to promote a science of affective styles in nonhuman animals and significantly advance research on animal welfare.

1. Introduction

Understanding and describing the subjective experiences of farmed animals is a major challenge in animal welfare research (Duncan, 1993). Subjective experiences are shaped by individual affective states, which are either pleasant or unpleasant, rather than hedonically neutral (Cannon, 1929). Animals appraise a situation based on the associated affective state and react accordingly. The term "affective states" comprises moods—the free-floating affect over the long term of an individual—and emotions—short-lived affective reactions directed towards a stimulus (Paul et al., 2005). Since affective states occur in the brain, for which direct investigations remain difficult in free-moving animals, indirect indicators have been developed in recent decades (Mendl and Paul, 2020). These indicators consist of measuring the behavioural, physiological and cognitive outputs that accompany changes in affect (the "componental view" of emotion; Paul et al., 2005). Since an individual's expectations modulate its affective state (Gygax, 2017), the

appraisal process is, in essence, individual (Lazarus, 1993). This may explain why, in the field of animal welfare, studying individuality in farmed and captive animals has also become an important focus point, especially to account for individual needs and to foster a concept of individualized welfare (Broom, 2010; Puppe et al., 2012; Winckler, 2019). An ideal framework to comprehend animal individuality is the study of personality, whose application is relatively recent in animal welfare research (Finkemeier et al., 2018). Personality refers to correlated behavioural and physiological patterns that are consistent over time and situations within an individual (Gosling and John, 1999; Réale et al., 2007). Surprisingly, research into both research topics (affective states and personality) does not seem to overlap yet (but see Asher et al., 2016). On the one hand, research on affective states has focused on the thoroughgoing study of different types of emotions (distress and fear, but also positive emotions) at the population level without addressing individual differences in emotional reactions. On the other hand, personality research often does not focus on the internal states at the origin

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of the behavioural outputs, even though most personality tests measure reactions to different types of affective (e.g., threatening or novel) stimuli. Indeed, individual differences observed in those tests are often assessed primarily based on behaviour and not on the other (cognitive or neurophysiological) components of an emotional reaction. Nevertheless, these components are an integral part of personality. At the moment, this seems to be acknowledged only in the concept of coping, which refers to the behavioural and physiological efforts to master a stressful situation (Koolhaas et al., 1999) and may represent a separate personality dimension (Finkemeier et al., 2018; Koolhaas and van Reenen, 2016; Zidar et al., 2017). Throughout this article, we will consider it as such. Extreme coping styles (i.e., high vs. low reactive) have been linked to distinct physiological reaction patterns of the hypothalamic pituitary adrenal (HPA) axis (Carere et al., 2010; Koolhaas et al., 1999; Roche et al., 2016) and the autonomic nervous system (Krause et al., 2017).

A promising approach that has the potential to help understand the interactions between personality and affective states is the study of laterality (asymmetries of brain and behaviour). In recent decades, this approach has gained interest and is currently considered a non-invasive way to study cerebral processing, e.g., the processing of affective states (Leliveld et al., 2013; Mendl and Paul, 2020; Rogers, 2009; Vallortigara and Rogers, 2020; Vallortigara and Versace, 2017; Versace and Vallortigara, 2015). Given that each hemisphere connects and controls the contralateral part of the body (Rogers et al., 2013), cerebral lateralization is reflected by the observation of motor and sensory side biases—i.e., behavioural lateralization. In this article, we focus on emotional lateralization, which refers to the fact that the two brain hemispheres differ in their specialization for processing certain types of emotions (MacNeilage et al., 2009). The study of emotional lateralization is promising for understanding how affective states and personality are integrated into an individual appraisal and their underlying cerebral processes. For this, introducing the framework of affective styles into animal welfare research could be insightful.

In human research, affective styles refer to consistent individual differences in emotional reactivity and regulation (Davidson, 1992). While emotional reactivity refers to the way (e.g., intensity or latency) that an individual responds to a stimulus, emotional regulation refers to processes "that serve to either amplify, attenuate, or maintain the strength of emotional reactions" (Davidson, 1998). Individual differences in cerebral lateralization are suggested to represent the origin of these affective styles (Davidson, 1992). Indeed, individual differences in hemispheric asymmetries during resting can predict both personality (for review see Coan and Allen, 2003) and individual differences in the intensity of specific affective reactions, i.e., affective styles (Davidson, 1998). The lateralization underlying human affective styles is widely acknowledged as a reliable biomarker of psychological well-being and psychopathology (Davidson, 2004; Grimshaw and Carmel, 2014). Therefore, studying affective styles in non-human animals may present equivalent potential for animal welfare research. Methods and techniques for investigating affective styles in humans include objective measurements of emotional reactions (e.g., by using neurophysiological indicators in real-time; Davidson, 2015) and repeated testing, which warrant the existence of stable traits and justify the term "styles". Such methods are also commonly used in animal welfare research. Thus, we believe it is time to investigate affective styles in non-human animals, which could represent an overarching theoretical framework for both the study of personality and individual differences in affective states and their link with cerebral lateralization.

This opinion piece aims to promote research on affective styles in non-human animals. As guidance for this article, Fig. 1 summarizes and combines all the central notions discussed. First, we present the current knowledge of the link between individual patterns in affect and in lateralization in non-human animals. After presenting the existing hypotheses on emotional lateralization, we discuss the experimental evidence from research on emotional reactivity, personality, and coping style in non-human animals supporting those hypotheses. Then, we
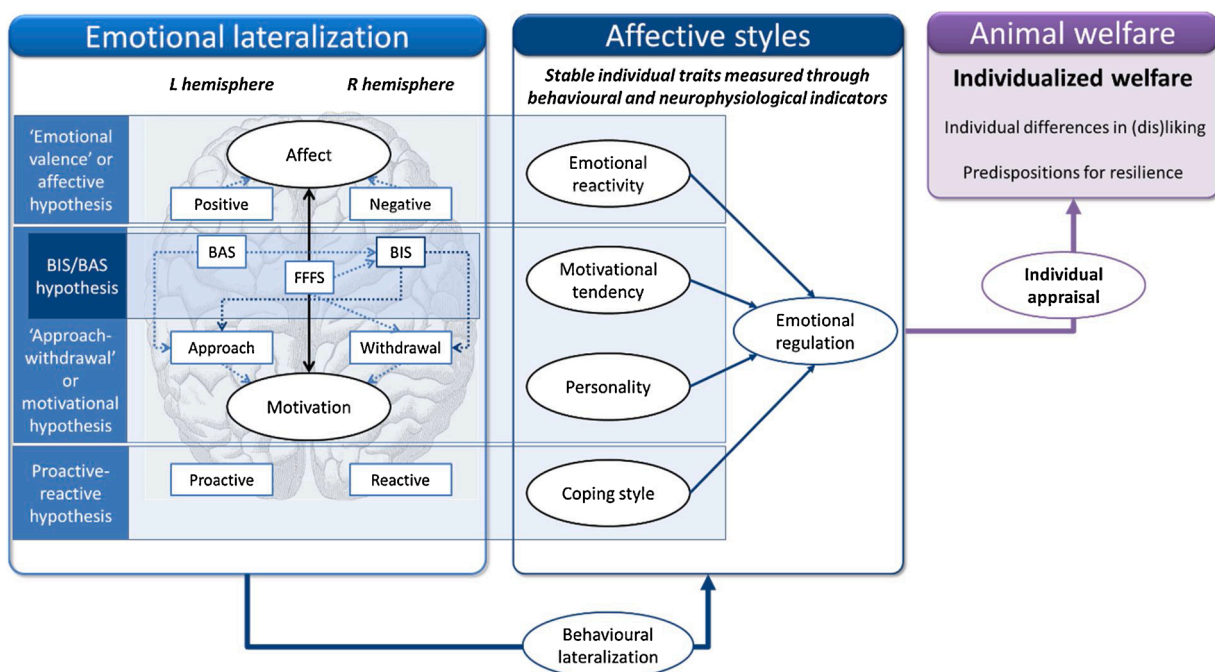
Fig. 1. Links between emotional lateralization, affective styles and animal welfare. Left box: Predictions of the different hypotheses on emotional lateralization and their link with internal states and behavioural outputs. The solid black line represents the feedback loop between core affect, motivation and the resulting behavioural outputs (Burghardt, 2019; Gygax, 2017; Mendl and Paul, 2020). Dotted lines link the predictions of each hypothesis (in rectangular shapes) to each proposed concept. Middle box: To start studying affective styles, we propose investigation of stable individual traits measured through behavioural and neurophysiological indicators of affect combined with an individual's hemispheric dominance (indirectly assessed through the observation of individual behavioural lateralization patterns). Right box: Implications for animal welfare through more insight into individual appraisal. R: right; L: left; BAS: behavioural activation system; BIS: behavioural inhibition system; FFFS: fight-flight-freeze system.

demonstrate that there are some limitations to the evidence and that we need to go beyond the current hypotheses and methods used in non-human animals. Due to the observed knowledge gap, we argue in favour of using lateralization to gain insight into individual appraisals. After this, we propose some guidelines to start the study of affective styles in non-human animals. Finally, we explain why we believe that the framework of affective styles could be promising to advance animal welfare research.

2. Current knowledge

Studying lateralization in the context of affective states might be confusing due to the existence of several hypotheses on emotional lateralization. However, these different hypotheses may explain distinct cerebral processes, each involving different neural structures (Killgore and Yurgelun-Todd, 2007; Schepman et al., 2015). In the following section, we will discuss four influential hypotheses that are illustrated in Fig. 1 (left box): the affective hypothesis (also referred to as the "emotional valence hypothesis"); the motivational hypothesis (also referred to as the "approach-withdrawal hypothesis"); the BIS/BAS hypothesis (BIS - behavioural inhibition system; BAS - behavioural activation system), which derives from the motivational hypothesis and specifically focuses on individual differences; and the proactive-reactive hypothesis. The right hemisphere hypothesis, which states that only the right hemisphere processes emotions, has been excluded from this article because it seems relevant only with regard to the expression and perception of emotions (Gainotti, 2018; Lindell, 2018) and not necessarily for appraisal processing. These hypotheses are mostly studied at the population level (by investigating which hemisphere is dominant in processing a specific emotion across the individuals in a population; e.g. in dogs: Quaranta et al., 2007; Siniscalchi et al., 2013, 2011) but can also be tested at the individual level (by investigating how individuals with different hemispheric dominance differ in their emotional reactivity, personality or coping style; e.g. in dogs: Barnard et al., 2018, 2017; Wells et al., 2017). This last point will be discussed in Section 2.2 (see also Fig. 1, middle box).

2.1. Hypotheses regarding emotional lateralization

The affective and motivational hypotheses (Fig. 1, left box) are very similar in their predictions. The idea that positive emotions or approach motivations are processed by the left hemisphere and that negative emotions or withdrawal motivations are processed by the right hemisphere arose with the publication of Schwartz et al. (1979). Based on this idea, many studies have amalgamated approach motivation with positively experienced emotions or avoidance motivation with negatively experienced emotions (for reviews, see Davidson, 2001; Demaree et al., 2005; Harmon-Jones and Gable, 2018; Ocklenburg et al., 2018). However, the predictions of the two hypotheses can differ for some emotions such as anger, which is a negative emotion involving approach motivation (Carver and Harmon-Jones, 2009; Harmon-Jones, 2004). Evidence relating to these hypotheses has been contradictory (for reviews, see Harmon-Jones, 2004; Harmon-Jones and Allen, 1998; Leliveld et al., 2013; Wager et al., 2003). Killgore and Yurgelun-Todd (2007) stated that several hypotheses might be true only at different cerebral levels and therefore could reflect "different facets of a complex distributed emotional processing system". For instance, the affective hypothesis may relate to the valence with which a particular stimulus/situation is experienced (the appraisal of a negative or positive core affect), while the motivational hypothesis may relate to the decision made to approach or avoid a stimulus/situation (Harmon-Jones and Gable, 2018), independent of the valence of this stimulus/situation (Harmon-Jones et al., 2013). Thus, instead of testing which hypothesis is true and which one is wrong, it may be interesting to choose the hypothesis to test according to which cerebral process is (supposedly) involved.

The two next hypotheses are especially well suited to investigate individual differences in emotional lateralization. First, the BIS/BAS hypothesis (Fig. 1, left box) is a refinement of the original motivational hypothesis based on the framework of the reinforcement sensitivity theory of personality (Gray, 1973; Gray and McNaughton, 2000). This theory describes three different neural systems that are responsible for the regulation of approach-avoidance behaviour. First, the fight-flight-freeze system (FFFS) is involved in punishment sensitivity: it controls the avoidance of aversive stimuli. Second, the behavioural activation system (BAS) is involved in reward sensitivity: it regulates approach behaviours. Finally, the behavioural inhibition system (BIS) becomes activated during approach-avoidance conflicts, namely, when the FFFS and BAS are in conflict. The BAS and FFFS are closely associated with approach and withdrawal behaviour, respectively, and were, therefore, originally expected to be regulated by the left and right hemispheres, respectively, based on the motivational hypothesis (Demaree et al., 2005; Gable et al., 2018; Harmon-Jones and Gable, 2018; Ocklenburg et al., 2018). However, recent evidence suggests that the BIS, rather than the FFFS, is regulated by the right hemisphere (Garrison et al., 2018; Lacey et al., 2020; Neal and Gable, 2019; for reviews see Gable et al., 2018; Harmon-Jones and Gable, 2018). Hence, the BIS/BAS hypothesis has been refined, stating that regulation of approach-avoidance conflicts (i.e., the BIS) is processed by the right hemisphere, while reward sensitivity (i.e., the BAS) is processed by the left hemisphere (Gable et al., 2018). In human research, testing the BIS/BAS hypothesis (combining the measurement of baseline hemispheric lateralization and motivational tendencies) has been a fruitful way to improve our understanding of individual differences in emotional reactivity and emotional regulation (Gable et al., 2018; Harmon-Jones and Gable, 2018) and therefore of affective styles. For example, greater involvement of the left hemisphere during positive appraisal has been shown to be predicted by a high BAS score (Balconi and Mazza, 2010), meaning that the BIS/BAS hypothesis might be crucial for understanding the link between affect and motivation. However, this hypothesis seems to remain human-exclusive as, to our knowledge, no methods to measure individual differences in motivational tendencies (such as a BIS/BAS scale, which is assessed by measuring reward and punishment sensitivities) have been developed yet in non-human animals.

Given that the right hemisphere intervenes in the physiological stress response involving the HPA axis (Ocklenburg et al., 2016; Rogers, 2010), it has been suggested that the left hemisphere controls proactive behaviours, while the right hemisphere controls reactive behaviours (the proactive-reactive hypothesis; Fig. 1, left box; Rogers, 2009, 2010). As a consequence, Rogers (2009, 2010) concluded that observing behavioural lateralization (e.g., hand preferences) should help identify individuals with a higher vulnerability to stress, which is important for animal welfare.

2.2. Experimental evidence

In this section, we first explain to what extent indirect (behavioural) measurements in individual lateralization patterns can be comparable with direct cerebral measurements used in research on affective styles. For this, we introduce the concept of individual hemispheric dominance. Based on empirical evidence, we then discuss how the different hypotheses on emotional lateralization may explain the link between individual motor lateralization patterns and individual patterns in affect (see Fig. 1, middle box).

Research on human affective styles seems to be exclusively based on direct cerebral measurements. As indicated in the introduction, baseline cerebral asymmetry is measured in humans as a trait (e.g., through repeated measurements during resting), and individual differences in those asymmetries are useful for predicting, e.g., resilient affective styles (Davidson, 2004, 1998). In non-human animal research, these methods are hardly implemented because they are still relatively invasive and resource-demanding, especially in freely moving animals (but see recent

development in horses: Cousillas et al., 2017; d'Ingeo et al., 2019; Rochais et al., 2018). Alternatively, Rogers (2009) suggested that the observation of individual motor biases in simple tasks may be a useful indirect method to assess individual differences in hemispheric baseline activities in non-human animals, a phenomenon also called "individual hemispheric dominance" (Kinsbourne, 1997; Wright and Hardie, 2015). The use of simple tasks is important because complex functions mostly require hemispheric specialization and are therefore less likely to be lateralized at the individual level (Fagot and Vauclair, 1991). Individual hemispheric dominance during simple tasks might therefore be a good approximation of hemispheric baseline activity measures in the context of affective style research, even though human affective styles have not yet been linked with individual motor lateralization patterns (e.g., left handers are systematically excluded from those studies; Coan and Allen, 2003). However, recent research in humans shows that hand preferences indicate a greater involvement of the contralateral hemisphere, at least in the motor control of the body (Grabowska et al., 2012; Packheiser et al., 2020; van den Berg et al., 2011). As a result, individual hemispheric dominance assessed through the observation of consistent side biases in non-human animals can be seen as an alternative to direct measurements of cerebral baseline asymmetries used in research on affective styles. Ideally, different types of motor functions should be observed to account for the multidimensionality of laterality (see our recommendations, section 3.2). Based on the hypotheses on emotional lateralization, individuals with opposite hemispheric dominance (i.e., with opposite consistent motor lateralization patterns) should differ in their personality, emotional reactivity, or coping style (Rogers, 2009).

At the present time, the only findings examining the link between emotional reactivity and lateralization have focused on moods, learned helplessness or behavioural despair. Left-biased individuals (assumed to have right hemispheric dominance) have been shown to be more pessimistic in cognitive bias tests (Gordon and Rogers, 2015; Marr et al., 2018; Wells et al., 2017) or more likely to show learned helplessness (Carlson and Glick, 1991) or behavioural despair (Ecevitoglu et al., 2020; Soyman et al., 2018) than right-biased individuals (assumed to have left hemispheric dominance), which is in accordance with the affective hypothesis. Thus far, however, emotional responses have not been tested for stability over time, which is a knowledge gap that has to be addressed to start research on affective styles in non-human animals (see our recommendations section 3.2).

As there are currently no standardized tests for assessing non-human animals with a BIS/BAS scale, there is also an obvious knowledge gap regarding the link between motivational tendencies and lateralization in non-human animals. An exception may be the study of Watson and Ward (1996), in which the authors extracted behavioural inhibition scores in small-eared bushbabies using a principal component analysis based on classic personality tests. This approach is in line with the idea that motivational systems are at the roots of personality dimensions (Gray and McNaughton, 2000). However, the results contradict the BIS/BAS hypothesis because left-handed small-eared bushbabies were less behaviourally inhibited than right-handed bushbabies (Watson and Ward, 1996). Since the authors found that left-handed subjects also showed greater activity, they suggested that left-handed individuals would be hyperactive rather than inhibited (Watson and Ward, 1996). In contrast, innovative horses with supposed higher inhibitory control have been found to be left-biased in their motor and sensory laterality (Esch et al., 2019). This would be in accordance with the BIS/BAS hypothesis. Human right handers show lower BIS scores than human left handers (Beaton et al., 2017, 2015; Wright et al., 2009, 2004; Wright and Hardie, 2012); these studies seem to contain the only reliable findings in humans showing differences in behavioural traits between left and right handers, as there have been no other proven links between personality dimensions and handedness (Grimshaw and Wilson, 2013). The BIS is hypothesized to play a crucial role in emotional regulation (Gable et al., 2018) because it is superordinate to approach (BAS) and withdrawal (FFFS) motivations (Gray and McNaughton, 2000): it can

mediate the BAS and FFFS or even suppress their activity. However, only a recent focus using innovative methods proved its role in emotional regulation (Lacey et al., 2020; Neal and Gable, 2019). Therefore, we believe that studying the BIS in non-human animals should also contribute to gaining insight into individual differences in emotional regulation.

Many studies in vertebrates have investigated the link between motor lateralization and particular personality traits. Most findings suggest that individuals with left hemispheric dominance are bolder and/or more explorative than those with right hemispheric dominance (Batt et al., 2009; Braccini and Caine, 2009; Cameron and Rogers, 1999; Fernández-Lázaro et al., 2019; Gordon and Rogers, 2010; Goursot et al., 2019a; Hopkins and Bard, 1993; Hopkins and Bennett, 1994; Larose et al., 2006; Rogers, 2018; for exceptions, see, e.g., Brown and Bibost, 2014). These findings support both the motivational and the affective hypotheses. Evidence also shows that right-biased individuals are more sociable (Gordon and Rogers (2010); Goursot et al., 2019a; Vaughan et al., 2019; Westergaard et al., 2004, 2003), more active (Barnard et al., 2017; Glick and Ross, 1981; Gordon and Rogers, 2010) or less aggressive (Anderson et al., 2010; Schneider et al., 2013; Siniscalchi et al., 2019) than left-biased individuals, but evidence remains contradictory (for activity: Chivers et al., 2017; Watson and Ward, 1996; for aggressiveness: Wells et al., 2019). However, repeatability in personality test results is rarely taken into account, even though this is considered an important aspect of personality (Dingemanse and Wright, 2020). Some exceptions include studies linking personality and laterality in fish that involved repeated personality testing (Brown and Bibost, 2014; Clotfelter and Kuperberg, 2007; Irving and Brown, 2013). Regarding mammals, Branson and Rogers (2006) found that ambilateral (i.e., without any side biases) dogs were shyer than left- or right-biased dogs when exposed to thunderstorms or fireworks noise. As the authors verified that the two playback tests were repeatable and that these findings correlated with a questionnaire noise score, their results are robust. Other examples of systematically repeated behavioural testing or observations are studies that found that macaques with right hemispheric dominance show more defensive aggression (Kalin et al., 1998) or received more aggression (Westergaard et al., 2004) than those with left hemispheric dominance. In section 3.2., we recommend following these few examples that accounted for repeatability in personality test results.

Regarding coping styles and lateralization, the available evidence has been inconsistent (Batt et al., 2009; Pereira et al., 2018; Vaughan et al., 2019; Westergaard et al., 2004, 2003, 2001, 2000). One problem is that reactive coping style is sometimes used as a synonym of stress vulnerability. This idea probably comes from the finding that reactive individuals show the highest corticosterone responses (Koolhaas et al., 2007). However, the proactive coping style cannot be considered by default less vulnerable than the reactive style. Moreover, it seems that definitions of coping are not standardized within and across species. For example, Barnard et al. (2018) found that dogs with a left bias showed "higher expression of stress-related behaviours, including frequent change of state, vocalisations, sitting, and low posture", and concluded that dogs with a right hemispheric dominance may show a more reactive coping style and might be more vulnerable to stress, as predicted by Rogers (2010). However, some of these behaviours have been found to be associated with a more proactive coping style in other species (e.g., frequent changes in state in pigs: Zebunke et al., 2017; vocalisations in marmosets: Gordon and Rogers, 2010). The consideration of coping as a stable trait in pigs has been recently criticized (O'Malley et al., 2019). However, we believe that this criticism is due to a lack of standardization regarding repeated testing (Zebunke et al., 2017, 2015; see our recommendations in section 3.2) rather than the lack of existence of coping as a trait.

Regarding farm animals, it seems that the investigations of the link between motor laterality and individual behavioural and physiological patterns to date have been restricted to the contexts of stress or health

(but see Esch et al., 2019; Goursot et al., 2019a; Larose et al., 2006). For example, strongly lateralized ewes were more stressed during a separation test (Barnard et al., 2015). Since coping can interact with general health and since motor laterality can reflect coping, it is not surprising to see that links also exist between motor laterality and immunity (Morgante et al., 2007; Quaranta et al., 2008, 2006, 2004; Siniscalchi et al., 2010) or disease likelihood (Zucca et al., 2011). In farm animals, there are some studies that have linked behavioural lateralization with health issues such as lameness or mastitis (reviewed by Leliveld, 2019). Thus, this observation shows that the potential for research on laterality in farm animals to understand individual appraisal needs to be more exploited.

This overview of current experimental evidence shows that despite the many studies on individual hemispheric dominance and its links with individual (affective) behaviours in non-human animals, it remains unclear how those individual behaviours are linked to individual appraisal and affective styles. Therefore, we are far from being able to reliably use individual hemispheric dominance as an indicator for affective predispositions in non-human animals, especially in farm animals that have been understudied in this context. To gain more insight into individual appraisal, there is an obvious knowledge gap in the study of motivational tendencies in non-human animals, although findings with humans greatly contribute to the understanding of individual appraisal and emotional regulation. Additionally, there is a need to repeat behavioural tests (to test for stable traits within individuals) and to add more components to the behaviour, such as cognitive and physiological measurements (to reliably interpret the responses as affective reactions). In the next section, we explain how to start research on affective styles in non-human animals and propose some future recommendations with a practical example for operationalisation.

3. How to start investigating affective styles in non-human animals

Based on the general definition by Davidson (2004, Davidson, 2001, Davidson, 1998, Davidson, 1992) that (human) affective styles refer to consistent individual differences in emotional reactivity and regulation, we propose extending the affective styles framework to animal welfare research. Research on affective styles in non-human animals should encompass the study of consistent individual patterns in affect associated with individual hemispheric dominance, as it likely underlies various aspects of consistent individual differences. It can be reasonably assumed that individual patterns in affect can lead to consistent individual patterns in emotional reactivity, motivational tendency, personality or coping, which all reflect individual patterns in emotional regulation (see Fig. 1). Therefore, to apply the affective styles framework, we need to extend our theoretical background with suitable hypotheses and take into account, in particular, repeatability, multidimensionality and the componential view of affect in their practical operationalization.

3.1. Applying the BIS/BAS hypothesis

There are some limitations of the hypotheses about emotional lateralization that have been studied thus far in non-human animals. First, the motivational and affective hypotheses seem to only describe emotional lateralization rather than to specify which exact mechanism is lateralized or to explain how those mechanisms give rise to affect or motivation (Grimshaw and Carmel, 2014). Second, the proactive-reactive hypothesis still lacks evidence because definitions and methodology in coping research seem to not yet be standardized, for example, regarding test repetition (Zebunke et al., 2017, 2015).

An ideal first step to go beyond the limitations of those hypotheses would be to test the BIS/BAS hypothesis in non-human animals. As previously mentioned, testing the BIS/BAS hypothesis (i.e., combining the measurement of baseline hemispheric lateralization with individual

BIS/BAS scores) has been a fruitful way to improve our understanding of individual differences in human emotional reactivity and regulation (Gable et al., 2018; Harmon-Jones and Gable, 2018). This hypothesis is specifically well suited for focusing on individual differences and might contribute to linking both the affective and motivational hypotheses while giving insight into the neural substrates at the origin of affective styles. For example, Kennis et al. (2013) reviewed fMRI studies on personality in humans and showed that higher BAS scores are associated with activity of the ventral and dorsal striatum and ventral prefrontal cortex in response to positive stimuli, while higher FFFS and BIS scores are associated with activity in the amygdala in response to negative stimuli. As these motivational systems (BIS, BAS and FFFS) are theorized to be the neural origins of the different personality dimensions (Gray, 1973; Gray and McNaughton, 2000), one should test for associations between motivational tendencies (e.g., BIS and BAS scores) and personality dimensions (see requirements for good BIS/BAS scales in Torrubia et al., 2008, 2001). For example, extraversion has been found to be associated with the volume of the medial orbitofrontal cortex, which is involved in the BAS, while neuroticism has been associated with structures involved in the FFFS (DeYoung et al., 2010). Another advantage of testing the BIS/BAS hypothesis is that in humans, it is supported both by direct and indirect (i.e., behavioural) evidence of cerebral lateralization and that it seems to explain the hemispheric asymmetries underlying differences in affective styles (Davidson, 2004) and motivational tendencies (Beaton et al., 2017; Wright and Hardie, 2015). Based on these results in humans, we argue that testing the BIS/BAS hypothesis within the framework of affective styles will deepen our understanding of individual appraisal and personality in non-human animals.

To our knowledge, a BIS/BAS scale has not yet been developed in non-human animals, which is a clear knowledge gap in animal welfare research and even in ethology. Developing BIS/BAS scales in non-human animals would be beneficial for understanding the mechanisms of behavioural control (Gygax, 2017). More generally, this would improve research on the neuroscience of personality in non-human animals. The neuroscience of personality is a new research field in non-human animals (Latzman et al., 2018; Padrell et al., 2020; Weiss, 2018), and its combination with objective behavioural measurements is only very recent (Fritz et al., 2020; Gründemann et al., 2019; Haley et al., 2012). We think that measuring motivational tendencies may improve objectivization, contribute to studying the neural substrates of personality and explore the multidimensional nature of personality in more species, such as farmed animals. Regarding lateralization of the BIS and BAS, such research may additionally help to bridge the gap in laterality research between human and non-human animals, which is also considered one of the future challenges for laterality research (Ocklenburg et al., 2020).

3.2. Implementing repeatability, multidimensionality and the componential view

There are several methodological aspects that need to be accounted for when studying affective styles and their link with individual hemispheric dominance. First, to be able to refer to "style" or "hemispheric dominance", it is important to test for stability across time (i.e., repeatability). Second, laterality and individual (affective) patterns (cf. personality) have a multidimensional quality. Third, using the componential view of affect (i.e., the combination of several types of indicators) is crucial for comprehending affective responses.

Regarding repeatability, the existence of stable individual traits in affect is the core aspect of research on affective styles; therefore, testing for repeatability is mandatory. When assessing affective responses and lateralized behaviours indicating hemispheric organization, we need to systematically verify that the measures we take are repeatable over time to prove that these actually represent consistent traits of an individual. We already highlighted that repeatability is not always addressed when studying the association of laterality with personality or coping (see

Section 2.2), and it will have to be considered in studies on emotional reactivity traits or motivational tendencies. A possible (easy) way to test for repeatable, individual patterns of emotional reactivity could consist of systematically assessing affective states (e.g., using heart rate variability) during individual tests (e.g., novelty tests). Regarding laterality indices, repeated testing of motor laterality seems to be generally acknowledged and applied in most studies, which is necessary to categorize individuals as left- or right-biased, to assess the strength of their lateralization, and to determine individual hemispheric dominance. However, repeatability of laterality tests is not always confirmed as it seems to be the case in fish research (Roche et al., 2020; Vinogradov et al., 2021). This becomes problematic when a widely used test over several decades, namely the detour behaviour test, appears to be not repeatable in different fish species (Roche et al., 2020). One should however keep in mind that repeatability can depend on sex, stimulus type and the amount of testing. For instance, Vinogradov et al. (2021) recently showed in a well-conducted study full repeatability of the detour test in female mosquitofish.

Regarding the multidimensionality of laterality, it seems unlikely that individual hemispheric dominance can be determined based on only one measure of behavioural lateralization, especially because lateralization patterns can change based on the task (Fagot and Vauclair, 1991). Indeed, individual biases involved in different motor functions are often not associated (Batt et al., 2008; Tomkins et al., 2010; Wells et al., 2019). In this case, it may be meaningful to combine them (e.g., by using a cluster analysis) to identify individuals with consistent motor biases across motor functions (Goursot et al., 2018). Combining different measurements of behavioural lateralization contributes to a more accurate overview of individual hemispheric dominance (Goursot et al., 2019a, 2018). Regarding the multidimensionality of stable individual traits, it seems that the number of studies accounting for this aspect is increasing in laterality research (Barnard et al., 2017; Goursot et al., 2019a; Grimshaw and Wilson, 2013; McDowell et al., 2016). When establishing new behavioural scales aimed at studying motivational tendencies (e.g., BIS/BAS scales), it is also necessary to account for the multidimensionality of motivation, i.e., for the existence of several motivational systems (e.g., the BIS, BAS and FFFS) and to test for associations with some personality dimensions (Torrubia et al., 2008, 2001).

Last, the methodological challenge of accounting for multidimensionality can be considered similar to that of using the componential view of affect (Paul et al., 2005). Affective states are often assessed using either behavioural, physiological or cognitive indicators. We advocate using not one but several indicators, ideally from all three domains, because this will often provide much more detailed and reliable insight into an individual's state (Goursot et al., 2019b; Gygax et al., 2013; Kovács et al., 2015; Krause et al., 2017; Leliveld et al., 2017, 2016; Reefmann et al., 2009). Specifically, some frequently observed behaviours can only be reliably interpreted when also looking at physiological responses, for example, to differentiate resting from apathy (Fureix and Meagher, 2015; Squibb et al., 2018). Similarly, in the case of laterality, it could be insightful to combine behavioural and cerebral components of lateralization (Ocklenburg et al., 2020). Ideally, individual hemispheric dominance should be verified using direct cerebral measurements, even if cerebral processes are not as easily accessible in non-human animals as they are in humans using electroencephalograms (EEG) or brain imaging techniques such as functional magnetic resonance imaging (fMRI). To our knowledge, only very few studies in macaques have measured stable individual cerebral lateralization patterns using EEG; however, they did not link those measurements to hand preferences (Kalin et al., 1998).

3.3. Practical example for operationalization

New experimental approaches need to be developed to operationalize the hypotheses laid out above to clearly differentiate between them. To illustrate the need for new experimental approaches, we discuss some findings from our research group. In two recent studies, we showed that pigs with a left motor bias in two independent tasks, indicating right hemispheric dominance, were bolder, more explorative and more sociable than pigs with a right motor bias/left hemispheric dominance (Goursot et al., 2019a, 2018). While these results support the motivational hypothesis, they may also be interpreted within the BIS/-BAS framework. Pigs with right hemispheric dominance touched the novel object less quickly and less often and were more vocally inhibited than pigs with left hemispheric dominance, which may originate from differences in BIS tendencies, as already suggested in human research (Gable et al., 2018; Wright and Hardie, 2015). In another study, we found that when pigs had an eye patch on the right eye (forced right hemispheric dominance in visual processing), they showed a less positive appraisal of a positively conditioned object than when they had both eyes open (Goursot et al., 2019b), which is in accordance with the affective hypothesis. As these pigs showed an orienting response when seeing the positive object, their reaction might also be interpreted as being regulated by the BIS, whose role is to activate attention and arousal (i.e., orienting) to interpret ongoing actions during approach-avoidance conflicts (Gray and McNaughton, 2000). However, our experimental approaches in both studies were not designed to specifically test the BIS/BAS hypothesis. Since the BIS/BAS hypothesis may explain both differences in pig personality and affective processing, it may serve to refine predictions of both the motivational and affective hypotheses instead of contradicting them. Testing this hypothesis, however, requires a specific test design, i.e., a BIS/BAS scale.

Developing a BIS/BAS scale requires developing tests measuring reward and punishment sensitivity. Individuals with a high reward sensitivity (high BAS scores) would show an increased motivation for reaching a reward, while individuals with a high punishment sensitivity (high FFFS scores) would show an increased motivation for avoiding punishment. Typically, the BIS becomes activated in a novel context when the BAS and FFFS are in conflict. Therefore, a way of testing BIS scores in farm animals could be a test in a novel environment where the individual is subjected to the presence of both a reward and a punishment, and its reaction is measured. To our knowledge, there is no test available in the literature where reward and punishment are simultaneously presented, but there may be several ways of testing BIS/BAS scores. For instance, individuals with a higher behavioural inhibition (high BIS scores) would show an increased latency to access the reward, while individuals with a lower BIS score would approach a reward more quickly, despite the presence of a punishment. Another way to test BIS would be to measure effortful control of motivation during a similar approach-avoidance conflict, where subjects' willingness to endure a punishment for obtaining a reward is tested (Lacey et al., 2020). For this, a possible experimental approach would be to measure the motivations of subjects to cross a corridor containing a punishment to subsequently access a reward. Subjects with high BIS scores would be able to endure the punishment longer to access the reward. BIS scores differ from FFFS scores, although they are often confounded (Corr and Cooper, 2016; Lacey et al., 2020): individuals with a strong punishment sensitivity (high FFFS scores) react more intensively (e.g., longer freezing duration) towards a punishment than individuals with lower FFFS scores. In contrast, strong reward sensitivity (high BAS scores) would be reflected by greater impulsive behaviour when accessing a reward. To establish BIS/BAS scales, it has also been recommended to combine them with classic personality dimensions (Torrubia et al., 2008, 2001).

4. The promises of research on affective styles for animal welfare

In this section, we discuss how the study of affective styles may benefit animal welfare (Fig. 1, right box). As previously discussed, applying the framework of affective styles in non-human animals would be promising for gaining more insight into individual appraisal. Understanding individual differences in appraisal would be a crucial step

for advancing animal welfare research towards more individualized welfare. Animal welfare research has developed indicators of affective states in farm animals, and according to the componential view of emotions, experimental approaches that combine cognitive, behavioural and neurophysiological outputs of an affective reaction should be preferred (Paul et al., 2005). In farm animals, repeated testing is also applied more frequently now in personality research (Finkemeier et al., 2019; Foris et al., 2018), while research on lateralized processing of affective states, associations between individual hemispheric dominance and individual patterns in affect is still at an early stage (Leliveld et al., 2013; Rogers, 2010). We encourage the wider use and combination of such approaches in the animal welfare community, which would also enable research on affective styles.

Similar to human research on affective styles, the study of affective styles in farm animals could allow the development of trait markers that vary with neurological vulnerability to depression and anxiety (Grimshaw et al., 2014), which could serve to identify individuals with a predisposition for poor welfare. For example, research in rats (but not in farm animals) has shown that left motor bias is associated with learned helplessness (Carlson and Glick, 1991) or behavioural despair (Ecevitoglu et al., 2020; Soyman et al., 2018), which both predict depression. On the other hand, animals with higher trait resilience might be identified. Resilience can be defined as the maintenance of high levels of well-being despite exposure to aversive events (Davidson, 2004, 1998). In farm animals, classifications based on side biases might be used to non-invasively distinguish individuals with different affective reactions during everyday situations or with respect to trait resilience. They could serve as a basis for answering similar research questions as previously addressed in coping style research, for instance, how they influence affective reactions that are relevant to everyday life (Krause et al., 2017), how they interact with the environment (Bolhuis et al., 2005a), personality traits (Bolhuis et al., 2005b) or behavioural flexibility (Bolhuis et al., 2004), and how they may be used to improve group management (Ruis et al., 2002, 2001).

Studying positive welfare is currently a highly topical issue in animal welfare research (Rault et al., 2020; Webb et al., 2019), which might also benefit from the affective styles approach, specifically, using the BIS/BAS framework. For example, greater involvement of the left hemisphere during positive appraisal has been shown to be predicted by high BAS scores (Balconi and Mazza, 2010) or by greater left hemispheric activity during baseline (Balconi et al., 2015). Combining studies measuring individual hemispheric dominance (Goursot et al., 2019a) with studies testing for differential hemispheric involvement during positive appraisal (Goursot et al., 2019b) would be a first step towards research on affective styles. For example, in Goursot et al. (2019a), we could have combined personality tests with heart rate variability and may have observed a stronger orienting response during the Novel Object test in shyer individuals. In contrast, in Goursot et al. (2019b), we could have tested whether personality differences predict differences in emotional intensity for lateralized presentation of a positive stimulus. Another possible next step would be to use brain imaging techniques to enable measurements of hemispheric baseline activity in non-human animals. These measurements could be used to observe actual qualitative and quantitative differences in brain structures that underlie behaviour. This might represent a meaningful way of investigating the neural correlates of individual behavioural lateralization patterns and of affective styles. For instance, neural reactions associated with hedonism are well described in domestic pigs using fMRI (Clouard et al., 2012; Coquery et al., 2019). However, neither the lateralization of those reactions nor the existence of individual differences in perceiving positive cues have been tested yet.

To conclude, the link between individual behavioural lateralization and personality, mood, or coping style has already proven its potential for animal welfare research. However, we propose a new theoretical framework to guide future research based on the concept of affective styles and emotional lateralization as its neurological basis, which has provided new insight into individual emotional regulation in humans. Specifically, testing the lateralization of reward and punishment sensitivities (i.e., the BIS/BAS hypothesis), may advance the study of stable individual traits in affective processing. This would lead to more insight into individual appraisal and could contribute to more research on psychological welfare in non-human animals.

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Declaration of Competing Interest

The authors declare no conflicts of interest.

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