



# In the Zone: Towards a Comparative Study of Flow State in Primates

Fay E. Clark

School of Psychological Science, University of Bristol

Email: [fay.clark@bristol.ac.uk](mailto:fay.clark@bristol.ac.uk)

**Citation** – Clark, F. E. (2023). In the zone: Towards a comparative study of flow state in primates. *Animal Behavior and Cognition*, 10(1), 62-88. <https://doi.org/10.26451/abc.10.01.04.2023>

**Abstract** – Flow is an altered state of feeling ‘in the zone’ when fully absorbed in a challenge and is associated with positive affective state (feelings). Despite almost five decades of research, Flow has not yet been recognized in non-human animals, despite repeated suggestions from animal researchers it could exist. Recent advancements in behavioral and neurophysiological indicators of experience in humans and animals make it more possible than ever to detect Flow in other species. In this article, I propose a framework for comparative Flow research on humans and great apes. I conserve the original nine-component definition of human Flow developed by Csikszentmihalyi and its three conditional components, but re-structure the six experiential components into three dimensions: Focus, Motivation, and Affect. I evaluate the evidence for each dimension and component in great apes, and how current human Flow methods may translate to great apes. If Flow state exists beyond our species, this has major implications. It would provide insight into the evolution of internally derived happiness and ignite more comparative research in the field of positive psychology. Second, knowledge of Flow or a Flow-like state in other species would inform the design of more effective enrichment and therefore promote higher captive animal welfare. I hope to spark new discussions among human positive psychologists, comparative psychologists, and animal cognition and welfare scientists, so that we may begin to conceptualize and recognize non-human Flow.

**Keywords** – Animal cognition, Challenge, Great ape, Happiness, Intrinsic motivation, Task

---

## 1. Flow in Humans

### 1.1 What is Flow?

Have you ever been so absorbed in an activity that you lost awareness of the outside world? Perhaps you lost track of time while playing a computer game or felt a sense of effortless enjoyment while painting. If so, you have probably experienced Flow. Flow is a “gratifying state of deep involvement and absorption that individuals report when facing a challenging activity and they perceive adequate abilities to cope with it” (EFRN, 2014). It was originally described in humans almost 50 years ago (Csikszentmihalyi, 1975), and has since become a hallmark of positive psychology (Csikszentmihalyi, 2014; Peifer & Engeser, 2021). Flow can be induced by participating in a wide range of challenges (synonymous with tasks or activities in the human literature). These challenges can be lone or social, serious or playful, sedentary or motor-physical (Csikszentmihalyi & Nakamura, 2018; Ensenger, 2021).

The capacity for humans to experience Flow appears to be universal across cultures, although Flow-inducing challenges differ cross-culturally (Moneta, 2004) and the characterization of Flow can differ across different types of challenge (Csikszentmihalyi, 2014). The likelihood of experiencing Flow

and its level (intensity) also varies between individuals; those with more ‘autotelic’ (internally driven) and less neurotic and anxious personalities are more likely to experience Flow (Csikszentmihalyi, 1997a; Baumann, 2021).

## 1.2 Components of Flow

It is widely agreed that Flow is characterized by nine components (original source: Csikszentmihalyi, 1990; further development: Nakamura & Csikszentmihalyi, 2002; Kawabata & Mallett, 2011). Three of these components describe the *conditions* needed for Flow to exist, and the remaining six components describe a participant’s subjective *experience* of Flow (Table 1).

**Table 1**

*Nine Classic Conditional and Experiential Components of Human Flow*

<b>Conditions Required for Flow (Conditional Components)</b>
(1) A balance between challenge level and participant skill level
(2) The challenge has clear goals
(3) The challenge provides unambiguous feedback
<b>How Flow is experienced by the participant (experiential components)</b>
(4) Extreme focus on the challenge at hand
(5) Awareness of one’s own actions
(6) A sense of control over the challenge
(7) A loss of self-consciousness
(8) A loss of sense of time

*Note.* Based on Csikszentmihalyi (1990); further development by Jackson & Marsh (1996); Nakamura & Csikszentmihalyi (2002); Kawabata & Mallett (2011); Abuhamdeh (2020). Note the term ‘challenge’ is used for consistency but is synonymous across human Flow and animal cognition literature with ‘task’ or ‘activity’.

## 1.3 What is the Significance of Flow?

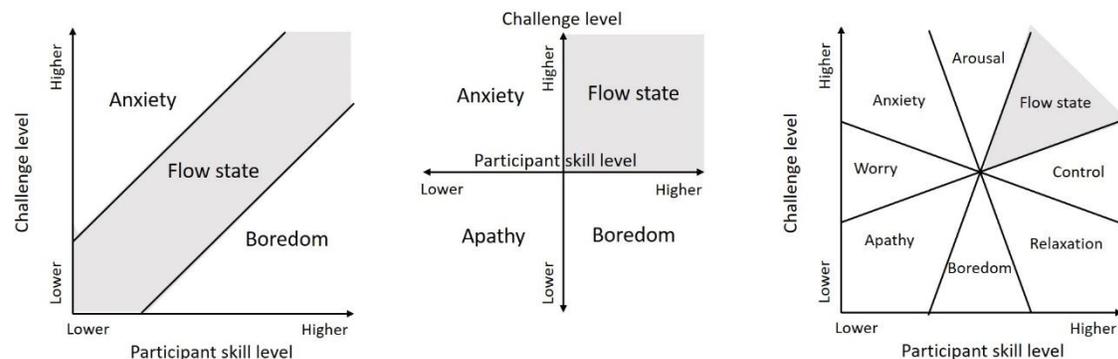
Csikszentmihalyi (1997b; 1999) proposed that ‘work’ (effort applied towards a challenge) is more likely to occur when it feels good, and therefore Flow is a tool to make work feel pleasurable or even relaxing. Therefore, from an evolutionary standpoint, Flow is associated with increased chances of survival through stress reduction, creativity, skill development, and peak performance. Crucially, Flow is not associated with extrinsic (external) rewards such as money, food, or prestige. The existence of Flow supports two different ways in which humans can derive happiness. The first is eudaimonic; happiness can be internally derived through personal growth and development and reaching one’s own potential by having autonomy (Deci, 1975; Ryan & Deci, 2001; Waterman, 1993). Related to this is the concept of self-actualization (Maslow, 1970, 1987). The second is hedonic; happiness can be derived from the pursuit of pleasurable feelings (Seligman, 2002; Vittersø & Søholt, 2011).

Despite Flow’s association with happiness, the more proximate link between Flow and affective state is complex (Abuhamdeh, 2021; Peifer et al., 2022). Positive affect is an integral part of Flow but paradoxically it does not feature as a classic component (Table 1). Rather than being an affective state itself, Flow is thought to *induce* feelings of pleasure, satisfaction, enjoyment, or relaxation (Csikszentmihalyi & Csikszentmihalyi, 1998). Interestingly, Baumann and Scheffer (2010) suggested that even though Flow is mainly associated with positive feelings, negative feelings can also be experienced during Flow, as a person alternates between ‘seeing difficulty’ and ‘mastering difficulty’ (Affective Change hypothesis; Baumann & Scheffer, 2010). It is also unclear whether the *process* of dealing with challenge (e.g., exploration and problem-solving) or the ultimate *outcome* of challenge (e.g., progression or solution) is associated with positive affect. Referring to an evolutionary perspective, it is unclear whether the good feelings associated with Flow exist to help us gain or improve a skill, reach a specific end goal, or both because the former is an antecedent and increases the likelihood of the latter.

Three major Flow models (Figure 1) illustrate the complex relationship between Flow and affect. We can visualize Flow as the ‘optimal experience’ arising when a participant’s level of skill matches the level of challenge (Csikszentmihalyi & Nakamura, 1989). In contrast, when skill and challenge are imbalanced, suboptimal experiences arise such as being under-challenged (boredom) and over-challenged (anxiety; also referred to as ‘overload’, see Figure 1). Therefore, Flow and negative affect can occur in close succession and share many characteristics like high focus (attention) on a limited stimulus field (Asakawa, 2010; Eysenck et al., 1992; Ullén et al., 2012).

**Figure 1**

*Three Models of Flow*



*Note.* Left: Three-channel model (based on Csikszentmihalyi, 1975). Middle: Four-channel model (adapted from Jackson and Csikszentmihalyi, 1999). Right: Eight-channel model (based on Csikszentmihalyi, 1975; Csikszentmihalyi & Nakamura, 1989). As model complexity increases from left to right, we see more nuance between the experience of positive and negative affect and can visualize more fluctuations between Flow and other states.

## 2. Is Flow Found in Animals?

Thus far, Flow state has never been reported in animals. So, could Flow be a uniquely human phenomenon? As stated earlier, human Flow has repeatedly been linked to skill acquisition and development in addition to happiness/well-being (Csikszentmihalyi & Nakamura, 2018). However, humans are not the only species to have a ‘technical brain’ (see Healy, 2021 for an examination of technology including tool-use driving the evolution of large brains), or to perform intrinsically motivated work associated with positive affect. We know animals can also be intrinsically motivated to work rather than pursue other activities (reviewed by Meehan & Mench, 2007; also see Clark & Smith, 2013; Langbein et al., 2009), work for food even when free food is concurrently available (contrafreeloading; Osborne, 1977), and experience pleasurable feelings when they are successful or at least progressing towards a goal (Hagen & Broom, 2004; McGowan et al., 2014; Perkins, 2000). Therefore, it seems feasible that the selection pressure/s for Flow could exist in other species.

A key characteristic of Flow is strong inner-world absorption (Table 1). This ‘tunnel-vision’ (Asakawa, 2010; Eysenck et al., 1992; Ullén et al., 2012) seems counterintuitive for wild animals because it comes at the expense of outer-world vigilance and gaining important (potentially life-saving) information about conspecifics, predators, and resources. However, total challenge absorption has been reported in laboratory primates. Markowitz and Line (1989) reported that rhesus macaques pressed a control switch over 100,000 times in one week to receive food rewards. Washburn and Rumbaugh (1992) found that rhesus macaques (*Macaca mulatta*) engaged with computerized challenges for over 9 h of their day. More recently, Guinea baboons (*Papio papio*) voluntarily used a computerized testing system *ad lib* that was available in their enclosure 24 hr per day. Eight out of nine individuals used it in very high frequencies, completing up to 1,800 trials per day (Fagot & Paleressompoulle, 2009). In these three published cases, the primates were

voluntarily selecting extreme challenge participation over other activities. So, there is a potential capacity, albeit maladaptive, for a high level of challenge absorption in captive animals.

Thus far, animal Flow has been proposed but not explicitly studied. Meehan and Mench (2007) briefly suggested Flow is a possible outcome of challenging captive animals but implied it has been overlooked because animal welfare scientists tend to concentrate on negative affect. Since then, Clark (2011, 2017) more explicitly proposed cognitive enrichment (i.e., challenges designed for evolved cognitive skills that, when worked, are associated with good feelings) as a conduit for Flow. In support of Clark's modular approach to cognitive enrichment (i.e., small, repeating units that can be scaled up or down to change the level of challenge), Nakamura and Csikszentmihalyi (2009) recommend that a (human) Flow challenge is graded and responsive so that it can accommodate growth in skill over time. Clark (2011) suggested Flow could logically be inferred in captive animals by how readily they are distracted from an engaging challenge, given the milieu of distractions in a typical enclosure. A decade later, Hintze and Yee (2021) proposed a practical vision for encouraging Flow in animals which focuses on offering intrinsic rewards. This leaves room for more fundamental evolutionary discussions about Flow in animals, and how we might initially work towards recognizing its existence.

### 3. A Proposal for Comparative Research

A comparative study of Flow (i.e., a comparison across humans and other species) requires a new comparative framework (Section 3.1) and a research paradigm to measure it (Section 3.2). My proposal is intentionally broad to suit comparative research across many taxonomic groups. I begin to narrow our perspective to great apes in Section 4.

#### 3.1 A New Comparative Dimensional Framework

I propose adopting the following human definition of Flow for comparative research: "Flow is a gratifying state of deep involvement and absorption that individuals report when facing a challenging activity and they perceive adequate abilities to cope with it" (EFRN, 2014). However, we should not expect to find all of Csikszentmihalyi's nine classic Flow components (Table 1) in animals. This is because Csikszentmihalyi (1990) drew his table from a wide range of human Flow experiences; they were never intended to be definitive inclusion criteria for Flow but somehow, they became used for that purpose in early research (Michailidis et al., 2018). Whereas some Flow researchers have continued to stick rigidly to the nine components and treat Flow as an all-or-nothing phenomenon (Cairns et al., 2014), most researchers do not (Peifer et al., 2022). So, if the nine components are rarely found together in humans, the same should be assumed for animals.

Are some classic components more common in human Flow than others and could we exclude some components altogether? This would be unwise; it is clear from existing Flow research there is a large variation in the presence and strength of components across individuals and types of challenge (Arzate & Ramirez, 2017; Csikszentmihalyi, 1990, 1998). For example, Sinnamon et al. (2012) suggested 'awareness of one's own actions' and 'loss of self' were irrelevant to Flow in musical challenges, whereas Swann et al. (2012) said that 'loss of self' and 'loss of time' had little significance in athletic challenges. However, a considerable number of Flow researchers have stressed the importance of 'challenge-skill balance' due to its high correlation with all other components; it has even been suggested that the dominance of challenge-skill balance makes Flow a uni-dimensional construct (reviewed by Norsworthy et al., 2021).

To facilitate a comparative study of Flow, we must acknowledge that the current, classic components of Flow lack operational value. Recently, several attempts have been made to re-structure Csikszentmihalyi's nine components into more accessible dimensions; for example, conditional *vs* experiential *vs* consequential (Engeser et al., 2021), or absorption *vs* challenge *vs* affect (Peifer & Engeser, 2021). Given that other complex psychological phenomena are modular or dimensional (Bräuer et al., 2020) it is reasonable to assume Flow is also multi-dimensional. But there is still no clear consensus on structuring and indeed, no attempts have been with a view towards comparative research.

I propose we maintain Csikszentmihalyi's (1990) clear distinction between *conditional* and *experiential* components of Flow (Table 1), and fortunately, the terminology is consistent with prior animal literature (i.e., challenge, skill, goals, feedback). So, to clarify, we will keep the three classic conditional components of Flow intact. In contrast, the experiential components of Flow need to be re-structured to allow consideration of logical 'dimensions' across species. I have restructured the traditional six Flow experiential components into three dimensions (focus, motivation, affect; Table 2). The interrelationship between cognition, motivation, and affect in humans and animals is already an established and active area of research (e.g., Dalglish & Power, 1999; Ford, 1992; Forgas, 2002; Kremer et al., 2020; Toates, 2004).

**Table 2**

*New Comparative Dimensions of Flow Experience*

<p><b>Dimension A. Focus</b>            1° Extreme focus on the challenge at hand (4)  <i>Additive components:</i>            2° Awareness of one's own actions (5)            2° A sense of control over the challenge (6)  <i>Subtractive components:</i>            2° A loss of self-consciousness (7)            2° A loss of sense of time (8)</p>
<p><b>Dimension B. Motivation</b>            The challenge is intrinsically motivating, i.e., without extrinsic reward (9)</p>
<p><b>Dimension C. Affect</b>            The challenge is associated with positive affect                During challenge                After challenge            2° Frustration may occur in brief succession with Flow</p>

*Note.* Numbers in brackets refer to the original experiential components of human Flow (Table 1). Focus is a primary (1°, most predominant) dimension of Flow and has four secondary (2°, less predominant) components nested within it.

### **3.1.1 Comparative Dimension A: Focus**

Many scholars argue that Focus (synonymous with concentration, attention, absorption), is the primary or most predominant dimension of the Flow experience (e.g., Asakawa, 2010; Eysenck et al., 1992; Ullén et al., 2012). Furthermore, it appears that secondary, less predominant or observable components can be nested within Focus. Flow is a complex phenomenon because it is both additive (a participant gains focus and control), and subtractive (a participant loses a sense of time and self). An increase in focus intuitively gives rise to a loss of time and loss of self because they are mutually exclusive processes. It could also be argued a loss of time and loss of self is equivalent to extreme focus on the challenge at hand, because a participant in Flow exchanges their awareness of the wider world, and their standing within it, for their awareness of and standing within the challenge. A loss of self-consciousness is a contentious Flow component (Norsworthy et al., 2021) and is often excluded in Flow surveys (questionnaires) because it does not correlate strongly with other components (Jackson & Marsh 1996; Nakamura & Roberts, 2016; Ullén et al., 2012).

### **3.1.2 Comparative Dimension B: Motivation**

A Flow challenge must be intrinsically motivating, in other words appealing to work on without an extrinsic reward (Table 1). The evolutionary basis of intrinsic motivation is beyond the scope of this paper but can ultimately be explained by organisms having a strong 'need' for sensory change (Hughes, 1997). Unlike Tordet et al. (2021), I have placed motivation and positive affect into separate dimensions. This is because motivation can come from positive (e.g., excitement) or negative (e.g., anger) states, so motivation is not always a 'positive' drive (Gable & Dreisbach, 2021). As we shall discover later (Section 3.2.2) the

intrinsic motivation characterizing Flow will make it difficult to study in traditional captive animal settings that use extrinsic food rewards.

### 3.1.3 Comparative Dimension C: Affect

As discussed in Section 1.3, there is a complex relationship between Flow and affect. At the ultimate level, we can talk about Flow and the evolution of happiness (eudaimonic and hedonic; Ryan & Deci, 2001; Seligman, 2002; Vittersø & Søholt, 2011). At a more proximate level, we can talk about affect in the form of short-term emotions, longer-term moods, and even longer-term affective states (Kremer et al., 2020). At this juncture, it is also worth noting the distinction between mood and what Bliss-Moreau and Rudebeck (2021) recently called ‘temporally extended affective states’ which they propose to be moods without conscious experience, i.e., in taxa without the capacity for consciousness.

As Flow research has progressed over almost five decades, many scholars have moved away from viewing affect as a mere consequence of Flow, to something that is integral to the experience itself (Abuhamdeh, 2021; Borderie & Michinov, 2016; Peifer & Engeser, 2021; Tordet et al., 2021). That is why I consider affect to be an important standalone dimension of Flow (e.g., Peifer & Engeser, 2021: absorption *vs* challenge *vs* affective framework) rather than merely a consequence (e.g., Engeser et al., 2021: conditional *vs* experiential *vs* consequential framework). Based on the human Flow literature, I believe it is necessary to make a distinction between positive affect *during* and *after* a Flow challenge (Table 2) because they are not necessarily going to be the same experience (Tordet et al., 2021). Considering affect at different points along a timeline fits with the modern ‘affective balance’ model of animal welfare, where short-term emotions and longer-term moods contribute to the overall balance of positive and negative affect (Kremer et al., 2020).

While Flow is most linked to positive affect, it has also been linked to negative affect, namely frustration or anxiety (Baumann & Scheffer; 2010; Borderie & Michinov; 2016; Tordet et al., 2021). For example, Borderie & Michinov (2016) asserted that participants in Flow state could become frustrated, and Kaye et al. (2018) observed mood fluctuations during Flow (note, it is more common in the literature to see *emotion* (short-term affect) associated with Flow, rather than *mood* (a longer-term state)). However, according to Flow models (Figure 1), anxiety/frustration is a neighboring state to Flow and it is likely a participant experiences frustration as they temporarily *leave* Flow when the challenge-skill level tips off balance (i.e., they encounter a higher level of challenge than their skill level can cope with; Figure 1). Thus, frustration and Flow are likely to positively correlate, but positive affect is a stronger indicator of Flow. Consequentially, I have included a statement in Table 2 that frustration may occur in brief succession *with* Flow.

## 3.2 Developing a Comparative Flow Research Paradigm

With a comparative dimensional framework of Flow in hand (Section 3.1) we can now think about an appropriate research paradigm. I will begin by considering the conditions and experiences of Flow, and end by justifying a computerized testing research paradigm.

### 3.2.1 Are Naturalistic or Experimental Challenges Better to Induce Flow?

Challenges can be considered as “opportunities for action”, so many opportunities in the world, naturalistic or experimental (induced, manufactured), can give rise to Flow (Csikszentmihalyi, 1990, p. 6). We must balance our desire to find Flow in animals with our ability to reliably and accurately measure what we find.

Human Flow was first identified outside the laboratory during naturalistic, self-pursued challenges that were not induced by a researcher such as playing musical instruments and rock-climbing (Csikszentmihalyi, 2014). Social challenges induce Flow in humans more frequently or more strongly than

lone challenges (Tiska & Engeser, 2021; Walker, 2010), but ‘collective Flow’ remains understudied (Norsworthy et al., 2021).

Like for humans, Flow might be induced naturally in animals when they pursue everyday activities and encounter challenges in their normal home environment (although it is important to remember Flow requires a level of work; it does not arise from very mundane activities; Csikszentmihalyi, & Csikszentmihalyi, 1998). Naturalistic observations of animals in zoos, sanctuaries, or the wild may allow us to capture natural, spontaneous Flow. Naturalistic challenges may have higher intrinsic value and clearer goals and feedback than ones designed in the laboratory. However, there is a tradeoff between more ecologically relevant challenges, and challenges we can design for multi-species comparisons under highly controlled conditions.

‘Computerized testing’ is the term I use hereon for a challenge displayed on a computer screen with responses via touchscreen or a joystick/button user interface (e.g., Harmat et al. 2015; Klasen et al., 2012; Ulrich et al., 2014). Computerized testing allows us to control the level, timing, and duration of challenge and record the participants’ behavioral and physiological responses at the same time. There are already two decades of digitized Flow research on humans to build upon (Peifer et al., 2022), and computerized testing has already been used to investigate the cognitive abilities of a range of species (Egelkamp & Ross, 2019; Kangas & Bergman, 2017; Seitz et al., 202; Washburn et al., 2017). Despite the popularity of computerized testing, it requires captive animals under at least moderately high control, so sample sizes and generalizability to an entire species are restricted. This being said, small sample sizes and limited generalization are prevailing problems across the field of animal cognition (Farrar et al., 2021) and human psychology (Kühberger et al., 2014) so should not deter animal Flow researchers. To counteract small sample sizes, experimental Flow research on humans tends to use a repeated measures design that tracks individual experience over time and different conditions (Abuhamdeh, 2020).

### ***3.2.2 Can We Overcome the Problem of Intrinsic Reward?***

The intrinsic motivation component of Flow is the most salient obstacle facing comparative research. Human participants will readily participate in psychological research trials with no extrinsic reward (sometimes participants will receive a small final reimbursement for taking part in a study but to my knowledge, this has never been classified as a true extrinsic reward). Conversely, captive animals are trained to participate in challenges using an extrinsic reward like food, water, toys, conspecific access, or tactile/ verbal reinforcement.

An extrinsic reward will undermine any intrinsic value of a Flow challenge (Deci et al., 1999), so this immediately precludes foraging and food-motivated challenges we typically use for enrichment and to test animal cognitive skills (Shaw & Schmelz, 2017; Young, 2013). Many animals can be intrinsically motivated to work on a challenge (Hughes, 1997), so the problem is not their capacity for intrinsic motivation but our ability to design creative experiments. Denying food rewards to animals who normally receive them (e.g., in laboratories and research centers) is not an option because it sends inconsistent learning cues that could place a long-term research project in jeopardy.

Instead, it may be possible to reward an animal for initially entering a test room and starting a challenge, but then no further extrinsic reward is offered for challenge engagement. Intrinsic motivation could be an emergent property of Flow (Csikszentmihalyi et al., 2005; Gold & Ciorciari, 2020), so a challenge that was initially extrinsically motivating could become intrinsically motivating over time. In support of this proposition, Clark et al. (2019) reported a Western lowland gorilla could extract nuts from a cognitive enrichment puzzle (it was designed to have a completion-contingent reward; Deci et al., 1999) but over time decided to store nuts in a pile rather than eating them.

### ***3.2.3 How Can We Balance Challenge and Skill Level in Animals?***

As discussed, many scholars believe ‘challenge-skill balance’ is the most important conditional component of Flow (reviewed by Norsworthy et al., 2021). Human Flow has been experimentally induced

by changing the level of a challenge in real time to match a participant's level of skill (Ulrich et al., 2014; Yoshida et al., 2014). Simple touchscreen challenges, such as touching or moving 2D shapes within a limited stimulus field, are ideal for this purpose because it is easy to quantify the level of challenge (Ulrich et al., 2014; Weber et al., 2017; Yoshida et al., 2014). So, we can easily satisfy the first classic condition for Flow (challenge-skill balance, Table 1) using computerized tasks.

If animals do not possess a requisite cognitive skill or cannot physically engage with a challenge due to their sensory and morphological adaptations, this will tip off the challenge-skill balance and induce frustration or anxiety (Meehan & Mench, 2007). Instead, if we prioritize the design of taxon-relevant challenges, we position Flow within the pre-existing framework of cognitive enrichment (Clark, 2022). As stated earlier, cognitive enrichment could be a conduit for Flow because it focuses on designing challenges that require evolved cognitive skills and can ultimately be overcome (Section 2). Of course, this raises a new issue for animal Flow researchers: can we design a task that is relevant to humans, and other species? Fortunately, animal cognition scientists have a wealth of experience modifying tasks for different taxa (Shaw & Schmelz, 2017).

Interestingly, some researchers have engineered one or two other experimental conditions to compare with the putative human Flow condition; a 'boredom' condition where participant skill exceeds challenge, and an 'overload' condition where challenge exceeds skill (Ulrich et al., 2014; Yoshida et al., 2014). The boredom condition may be analogous to what Unsworth & Robison (2018) refer to as a state of low arousal and low focus called 'mind-wandering'. In further support of setting up two alternative experimental conditions to Flow, there is an inverted U relationship between physiological arousal and Flow (Peifer & Tan, 2021), such that Flow is characterized by physiological responses intermediate between overload (high arousal) and boredom (low arousal). The same experimental approach is feasible for animals and there is growing research in the field of animal boredom (Burn, 2017); however it will require special ethical consideration (Section 7.3.3).

### ***3.2.4 How Can We Provide Animals with Clear Goals and Feedback?***

Human participants can be given quick written or verbal instructions for experimental challenges, but this is not possible for animals. Imagine a scenario where the goal of a challenge 'navigate a ball through a maze' is ambiguous. There are a number of ways we could provide animals with a clear challenge goal. Or we could transfer an animal's prior knowledge of moving objects past obstacles to a new maze task. A human or conspecific could demonstrate the goal response to the animal (social learning). Or, the animal's response could be gradually shaped using iterations of the challenge that get progressively more difficult. Another option is to allow the animal to respond spontaneously, but this does not provide a clear goal. In humans, we know that a human needs to come to the challenge equipped with some level of skill (Csikszentmihalyi & Csikszentmihalyi, 1998) so prior animal training seems permissible if it provides clear goals and skill. However, I also believe that spontaneous skill development in Flow is an important avenue of research given the link between spontaneous skill development and animal positive affect (Hagen & Broom, 2004).

### ***3.2.5 A Computerized Experimental Challenge Paradigm***

I propose we attempt to experimentally induce Flow in animals under highly controlled experimental conditions, using a computerized challenge paradigm. In summary, a computerized challenge paradigm will allow high levels of challenge responsivity and the ability to instantly log participant responses. Every effort should be made to remove extrinsic reward from this type of challenge. Three experimental conditions (putative Flow, boredom, and overload) should be attempted and are characterized by different levels of challenge-skill.

## 4 Evidence for Flow in Great Apes

The most logical place to begin comparative Flow research is within the primate order. Namely great apes (chimpanzees, *Pan troglodytes*; Gorillas, *Gorilla* spp., Orangutans, *Pongo* spp., and Bonobos, *Pan paniscus*), due to their close cognitive, physiological, and affective similarities to humans. A phylogenetic approach also allows for a progressive, step-wise expansion of research to less-related taxa in the future (MacLean, 2016). Comparative Flow research needs to be carefully ordered and structured. In this Section, I review the evidence for conditional and experiential components of Flow in great apes as well as their neurocognitive capacity, and therefore the holistic likelihood they have the capacity for Flow.

### 4.1 Conditional Components of Flow in Great Apes

#### 4.1.1 Balance Between Challenge and Skill

A balance between challenge level and skill level is important for great ape challenge performance and positive affect. In experimental studies of great ape cognition, the level of challenge (i.e., computerized task ‘difficulty’) has been manipulated primarily to investigate the limits of their cognitive skill, but also the impact of challenge level on affective state. Captive great apes perform more self-directed behavior (an indicator of anxiety) during a more difficult digital challenge (Leavens et al., 2001, 2004; Yamanashi & Matsuzawa, 2010) or when they make errors in a challenge (Itakura, 1993; Laméris et al., 2022a; Wagner et al., 2016; Yamanashi & Matsuzawa, 2010). Performance on a challenge also increases with challenge experience (Altschul et al., 2017; Massen et al., 2013), showing natural drift in challenge-skill balance. The importance of maintaining a challenge-skill balance for great apes is also evidenced by their rapid habituation to environmental enrichment (Brent & Stone, 1996; Clark, 2011; Padrell et al., 2022). For example, Clark (2011) found that great apes lose interest when enrichment items did not respond or evolve with repeated use.

#### 4.1.2 Clear Challenge Goals and Feedback

A clear understanding of what a challenge entails is important for great apes, in terms of their performance and affect. The performance errors of great apes described above (Section 4.1.1) were interpreted as responses to the apes’ perceived challenge-skill balance, but could also be explained as their responses to unclear challenge goals. In further support for the importance of predictability, or at least the absence of ambiguity, Perdue et al. (2014) found that rhesus macaques and capuchin monkeys (*Cebus* spp.) preferred to choose the order of computerized tasks they received, *versus* a random order of tasks. Great apes perform more self-directed behavior when there is no reward compared to an extrinsic reward (Itakura, 1993), or when there is a delay between response and reward compared to no delay (Elder & Menzel, 2001; Rosati & Hare, 2013). Great apes also respond less positively to an inequitable reward, such as receiving a lower quantity of reward food than a conspecific (Bräuer et al., 2006; Brosnan et al., 2010).

### 4.2 Experiential Components of Flow in Great Apes

#### 4.2.1 Focus in Great Apes

Flow is associated with the ‘addition’ of extreme challenge focus, self-awareness, and control (Table 2). Evidence of these cognitive abilities in great apes is mixed. Anecdotally, I have observed great apes interacting with cognitive enrichment with a deep sense of absorption (Clark, F.E., unpublished data), but this has never been empirically tested. Apes have the ability to control what they pay attention to, in spite of distractions, and this is deemed to be a form of higher cognition (Völter et al., 2022). In chimpanzees, attentional control has been demonstrated using a foraging puzzle; in the presence of sudden,

distracting noise the maintenance of attention was similar to that of 3-year-old children (Hermann et al., 2015). However, great apes show reduced performance on other cognitive challenges in the presence of social and non-social stimuli (Lam eris et al., 2022b).

Chimpanzees appear to get absorbed by the act of social grooming (Foster et al., 2009), but more research is needed to confirm how focused they are (and indeed whether social grooming is an example of ‘collective Flow’; Norsworthy et al., 2021). Stereotypical behavior (i.e., invariant, repetitive, non-functional behavior; Mason, 1991) could be another behavior requiring a high level of attention, but this is poorly understood. While stereotypical behavior is prevalent in captive great ape populations (Birkett & Newton-Fisher, 2011; Ferdowsian et al., 2011), and has similarities to obsessive-compulsive disorder in humans (Ferdowsian et al., 2011), it is not clear whether a subject is consciously focused on the stereotypical behavior at hand or rather in a state of low arousal and mind-wandering (Unsworth & Robison, 2018). In terms of control, great apes can monitor their own level of performance in a challenge, evidenced by making relatively ‘more confident’ or ‘less confident’ actions in a computerized memory task (Beran et al., 2015), and having an awareness of their own cursor movements in a computer task (Kaneko & Tomonaga, 2011).

Human Flow is also associated with a ‘loss’ of self and time (Table 2). Great apes are able to perceive time passing, as shown by their performance in delayed gratification tasks (Beran et al., 1999; Beran & Evans, 2006). Furthermore, Dufour et al. (2007) investigated the abilities of chimpanzees to cope with increasing waiting time for a food reward and found they can anticipate a delayed reward of several minutes. A loss of self is more difficult to evidence; great apes share the foundational social cognitive mechanisms of theory of mind with humans (Krupenye & Call, 2019) and therefore somewhat have a perception of ‘self’ that may subsequently allow a loss of self. However as discussed (Section 1.2), the subtractive components of Flow are more contentious than the additive components and I believe we should concentrate more on the primary components of Focus than the subtractive components (Table 2).

#### ***4.2.2 Motivation in Great Apes***

There is good evidence great apes will work on challenges with no extrinsic reward. For example, chimpanzees have shown high interest in or preference for cognitive enrichment that does not contain food rewards (Clark & Smith, 2013; Padrell et al., 2022) and wider environmental activities with no foraging context at all (Yamanashi et al., 2022). Altschul et al. (2017) found that chimpanzees scoring highly on the personality factor ‘openness’ continued to participate in a challenge when not rewarded with food, and Clark et al. (2019) also found inter-individual differences in gorilla motivation for extrinsic (food) rewards. Ebel and Call (2018) suggest the presence of food rewards distracts apes and delays their problem-solving performance; this is supported by a wider meta-analysis on intrinsic and extrinsic motivation (Deci et al., 1999).

#### ***4.2.3 Affect in Great Apes***

The link between positive affect and challenge in great apes was reviewed above to support the importance of challenge level (Section 4.1.1). Further to this, great apes show more general shifts towards more positive and/or species-specific behavior when they undergo periods of environmental challenge (Clark & Smith, 2013; Morimura, 2006; Padrell et al., 2022; Yamanashi & Hayashi, 2011; Yamanashi et al., 2016). An interesting study by Marzouki et al. (2014) demonstrated the impact of prevailing mood on primate cognitive processing: Guinea baboon response times on a computerized cognitive task were slower when their mood was negatively valenced, *versus* neutrally or positively valenced. This finding supports the Affect as Information hypothesis originally developed in humans (Schwarz & Clore, 2003). Research is increasing to show great apes have rich affective experiences across many aspects of their lives (Kret et al., 2020) and I will review the measurement of such affect in Section 6.

### 4.3 Neurocognitive Mechanisms in Flow

Flow research has always focused on subjective experience, but over time researchers have increasingly explored the potential underlying neurocognitive mechanisms. A comparative examination of human and great ape brains and nervous systems may, therefore, point towards the existence of requisite neural and cerebral architecture for Flow in great apes. The most supported neurocognitive model, the Transient Hypofrontality hypothesis (Dietrich, 2004) explains Flow as a transient state of downregulation of high cognitive control, and a transition from explicit to implicit information processing. In simpler terms, the brain moves from less controlled to more automatic functioning during Flow (Dietrich, 2004). Great apes possess an explicit system and therefore higher cognitive control somewhat similar to humans (Russon, 2004; Semendeferi et al., 2001), and therefore possess the system that is specifically ‘turned down’ when to individual enters Flow. An alternative neurocognitive theory, the synchronization theory (Weber et al., 2009) suggests Flow is associated with higher activity in the frontal executive parts of the brain, but there is less support for this theory (reviewed by Gold & Ciorciari, 2020).

### 4.4 Summary of Evidence for Flow in Great Apes

Overall, there is a moderate empirical basis for Flow in great apes. The three conditional components of Flow appear to be important for great apes, both in terms of challenge performance and affective state. Great apes also possess the underlying neurocognitive mechanisms to downregulate executive or higher-level cognitive processes in favor of more basic, automatic processes, which typify human Flow.

Unfortunately, there are gaps in our knowledge regarding the experiential components of Flow that might exist in great apes. Research on their level of focus (attention, concentration) is lacking; there is limited evidence for the focus (attentional) abilities of great apes in the context of experimental challenges from one study on attentional control during an auditory distraction (Hermann et al., 2015). So, it is difficult to predict the limits of great ape focus during Flow in our computerized testing paradigm. The extent to which great apes might lose a sense of time or self during challenge has not yet been investigated to my knowledge. Going forwards, the study of Flow in great apes needs to place particular emphasis on experiential measurements (Section 6).

## 5. Flow Measurements in Humans

In this section, I review how Flow has been measured in humans to date. Then, Section 6 will consider suitable comparative methods. There have been two main approaches to studying Flow in human participants: retrospective self-reporting (questionnaires), and concurrent (aka online) behavioral and neurophysiological measures. After decades of reliance on retrospective surveys, there has been a gradual shift toward direct behavioral observations and neural and physiological responses in humans.

### 5.1 Self-reports

Flow is a subjective state experienced by the individual, so in early Flow research, participants self-reported their experiences using a retrospective questionnaire (Csikszentmihalyi, 1990; Csikszentmihalyi & Csikszentmihalyi, 1998). Over ten questionnaires have been developed to date (Harris et al., 2021; Novak et al., 2000), the most common being the Flow State Scale (Jackson & Marsh, 1996) with 36-questions covering all nine Flow components. The Experience Sampling Method is also retrospective, and participants are summoned by a pager or computer pop-up window to answer questions at random points during a specific challenge or their daily activities (Hektner et al., 2007).

Self-report methods are increasingly losing favor in Flow research (Tordet et al., 2021). They rouse participants from the very state we are trying to measure, and questionnaires are fundamentally incompatible with Flow state because they require a deep level of introspection (Weber et al., 2017). Flow

state scales do not work well for children or those with communication difficulties (Inal & Cagiltay, 2007), and self-reports are subject to biases in reporting and memory (Killi, 2006; Redelmeier & Kahneman, 1996).

## 5.2 Behavioral Indicators

Human Flow research was built on a foundation of retrospective self-reports, which explains a relative lack of validated behavioral indicators. However, some Flow studies have looked for behavioral indicators in children because of their limited ability to understand or respond to questionnaires (e.g., Addressi et al., 2015; Custodero 1998). For example, Custodero (1998) made descriptive observations of ‘challenge-seeking’, ‘challenge-monitoring’, and ‘awareness of others’ while children participated in music classes. Finding that challenge-seeking and monitoring increased during Flow whereas awareness of others decreased. More recently, standardized and reliable ‘Flow observation grids’ have been developed which allow behaviors to be scored on point scales (Borderie & Michinov, 2016; Tordet et al., 2021).

## 5.3 Neurophysiological Indicators

Over the past two decades, many techniques have been used to investigate behavioral and physiological responses during Flow. I will briefly summarize the literature, but several comprehensive expert reviews are available (Harmat et al., 2015; Harris et al., 2017a; Nah et al., 2017; Peifer & Tan, 2021; Peifer et al., 2022).

Measures of brain activity (e.g., electroencephalography, EEG; and functional magnetic resonance imaging, fMRI) have been used to show Flow is associated with a de/activation of key human brain structures (Alameda et al., 2022). For example, Flow is associated with a temporary reduction in higher cognitive functions (Dietrich, 2003, 2004), specific activations of structures responsible for goal-directed attention and reward, and deactivations of structures responsible for self-conscious control of movement (Sanchez-Vives & Slater, 2005; Weber et al., 2009). Flow has also been linked to a loss of threat detection (Peifer, 2012) and dopamine reward pathways which implicate the importance of intrinsic motivation (de Manzano et al., 2013; Di Domenico & Ryan, 2017). Recent human research also shows some scope for inducing Flow using a non-invasive brain stimulation method called transcranial direct current stimulation (tDCS) (reviewed by Gold & Ciorciari, 2020).

Flow is physiologically stimulating (de Manzano et al., 2010; Harmat et al., 2015) even though it subjectively feels ‘effortless’ (Harris et al., 2017b). There is a curvilinear relationship between Flow and physiological arousal in general (van der Linden et al., 2021) as well as specific measures like cortisol (Peifer et al., 2011, 2015) and heart rate variation (de Manzano et al., 2010; Keller et al., 2011). Changes in how well the skin conducts electricity, known as electrodermal activity, is a relatively rapid indicator of general arousal and sympathetic nervous system activation in humans under challenge (Dawson et al., 2007). Electrodermal activity has been found to increase in some but not all Flow experiences (Kivikangas, 2006; Nacke et al., 2010), pointing toward the need for more research across different types of challenge (Peifer & Tan, 2021).

Subtle movements of facial muscles surrounding the eye and lips are linked to emotional valence in humans and have therefore been employed in Flow research (reviewed by Larsen et al., 2008; Peifer & Tan, 2021). Relative activity of the ‘frowning’ and ‘smiling’ muscles of the face, in addition to the muscle of the eyelid, have been implicated in Flow state albeit with inconsistent results that may reflect differences in Flow across activities and that speaking during the challenge can confound the data (Kivikangas, 2006).

Finally, eye measurements can be incorporated into human Flow research. Pupil dilation is an indicator of both general arousal and cognitive workload and follows the same inverted U curve discussed earlier (Section 5.3), such that pupil diameter during Flow is intermediate between boredom (small diameter) and overload (large diameter) (Bailey & Iqbal, 2008; van der Linden et al., 2021). Blink rate shows a similar pattern, midway between boredom (high blink rate) and overload (low blink rate) (Oh et al., 2012). Gaze direction and eye fixation have also been used to indicate the attentional components of

Flow. For example, optimal attention characterized by a period of eye fixation preceding movement (‘quiet eye’) is positively correlated to Flow (Harris et al., 2017c). Flow is also associated with longer durations or lower frequencies of focused gaze (Cheng, 2014; Ko & Ji, 2018), whereas boredom is associated with a deviation in gaze from a narrow field of focus (Kim et al., 2018). Eye measurements can be obtained from participants wearing eye-tracking glasses, headsets, or by coding video footage of the face. Pupillometry and eye tracking are increasingly being used on great apes to assess attention and autonomic (i.e., involuntary) responses (reviewed by Hopper et al., 2021; Kuraoka & Nakamura, 2022).

## 6. Comparative (Human-Great Ape) Flow Measurement and Evaluation

### 6.1 Self-reports

The fact we cannot ask animals to self-report is not a deal-breaker for comparative Flow research for several reasons: prevailing issues with Flow questionnaires, behavioral indicators of Flow already designed for humans, and increasing neurophysiological measures of Flow. In fact, not using self-reports drives Flow research forwards because it encourages the development of alternative methods targeted toward emotional valence and arousal, and nervous system activation.

### 6.2 Behavioral Indicators

Behavior is the most common and well-validated indicator of great ape cognition and affect (Kret et al., 2020; Russon, 2004). In great apes, voluntary task participation by non-deprived individuals could be used as a behavioral proxy for what Custodero (1998) refers to as ‘challenge-seeking’ but could also be described as intrinsic motivation. Custodero’s ‘challenge monitoring’ may be fairly intuitive for animal Flow researchers, based on the animal’s head and body orientation and how confidently they make actions (as opposed to pausing or working slowly).

Head and body movements can also be triangulated with eye measurements (Section 6.3). Nielson et al. (2005, p. 33) provide a useful definition of human behavioral repetition that would translate to great apes: “...the subject... had to (1) perform the same action at least four times, (2) without exhibiting an alternative action, and (3) without stopping the repeated action for any longer than 3 s”.

Behavioral indicators of positive and negative affect are highly taxon-specific but have been relatively well-validated in great apes (Birkett & Newton-Fisher, 2011; Ferdowsian et al., 2011 and the reply by Rosati et al., 2013; Kret et al., 2020; Nieuwburg et al., 2021). Indicators of negative affect include self-directed or other abnormal or injurious behavior; whereas exploration, play, or otherwise ‘normal’ behavior can be used to indicate positive affect. In animal affect research, the ambiguity of the term ‘normal’ behavior can cause difficulties; it can refer to behaviors that are common for the species, behaviors that are functional, or behaviors that are judged to be wild-like (Browning, 2020). My preference is always for promoting functional over naturalistic behavior in captive animals. We should focus on scoring positive behaviors which have the strongest validation against other measures, and the absence of stereotypical behaviors to indicate positive or at least neutral affect (Kremer et al., 2020). A Flow observation grid should be developed specifically for great ape behavioral indicators of Flow, with an appropriately devised scoring system based on pilot observations. For example, Tordet et al. (2021) used human pilot observations to justify scoring focus (what they called concentration) on a 5-point scale and enjoyment on a 4-point scale because there were fewer graded variations in the latter.

It is important to recognize that prevailing mood can affect primate cognition and *vice versa*. For example, negative mood can result in slower cognitive processes (Marzouki et al., 2014; Schwarz & Clore, 2003) and conversely, problem-solving impacts affect (e.g., Leavens et al., 2001, 2004; Yamanashi & Matsuzawa, 2010). Therefore, it will be necessary to record the precise sequences in which mood states (using valenced behaviors as a proxy) and task progression (solution, failure, progression) occur to elucidate their cause-effect relationships.

### 6.3 Neurophysiological Indicators

fMRI methods have been established for great apes due to their neuro-anatomical and physical similarities to humans (reviewed by Kuraoka & Nakamura, 2022), so it is feasible we can compare the brains of humans in Flow with great apes in suspected Flow. Brain waves have been obtained from electrodes placed on the scalp surface (not penetrating the skin) of a chimpanzee viewing affective and neutral photographs (Hirata et al., 2013). This method might provide an alternative to fMRI, but the animal needs to be kept still and placed in a highly unnatural situation so this will only be possible for a few case studies using artificially reared animals.

The measures of physiological arousal used in human Flow research (Section 5.3) have been somewhat established for great apes. For example, heart rate has been collected from chimpanzees by placing sticky electrode pads to their bare skin during stimulus exposure (Berntson & Boysen 1989; Boysen & Berntson, 1986). Saliva samples are commonly used to derive the short-term cortisol levels required for Flow research; these can be obtained by subjects chewing on a substrate to deposit the sample (Behringer et al., 2014, 2022; Elder & Menzel, 2001). In contrast, fecal glucocorticoids, while well-validated for great apes (Novak et al., 2013) provide a far longer-term measure of cortisol so may not detect cortisol changes due to Flow.

Electrodermal responses to valenced stimuli have thus far been validated in rhesus macaques (Amiez et al., 2003; Laine et al., 2009), but does not appear to be a common method for great apes. Body and facial temperature do not appear to be well-cited measures of human Flow, but have conversely been used in studies of great ape arousal using infrared thermal imaging (Kuraoka & Nakamura, 2022; Ross et al., 2021). For example, nasal temperature significantly dropped in chimpanzees exposed to emotionally valenced stimuli (Kano et al., 2016); and similarly, the temperature surrounding the nose and eye of gorillas varied with conditions of positive and negative valence (Chotard et al., 2018). Temperature can also be taken from the ear or finger (Parr, 2001; Parr & Hopkins, 2000).

In great apes, facial expressions (or more appropriately ‘facial behavior’ because facial muscle activation is not always linked to emotional state; Waller et al., 2020) have been fairly well studied and the facial action coding system (FACS) is available for chimpanzees and orangutans to quantify their facial behaviors from video footage. It may be possible to employ FACS as an indicator of emotional valence in chimpanzees (Fernández-Carriba et al., 2002). Waller et al. (2014) found no indication of ‘determination’ in the facial behavior of chimpanzees (in contrast to children) when trying to open a permanently locked food box. Rather, the chimpanzees’ levels of self-directed behavior decreased as challenge persistence increased. A similar result was observed by Clark & Smith (2013) who observed that exposure to a new cognitive challenge was associated with increased self-directed behavior in chimpanzees, but the behavior decreased when challenge participation increased.

Pupil changes and eye movements can be monitored in great apes wearing headsets (which can also measure hand, eye, and head coordination; Kano & Tomonaga, 2013), or using an externally mounted camera pointed at the face (Kano & Tomonaga, 2009). Pupil dilation in chimpanzees has recently been linked to engagement in social activities (Hepach et al., 2020) and paying attention to complex animations (Sato et al., 2021).

### 6.4 Further Experimental Design for Focus

The Focus dimension has the least empirical basis in great apes (Section 4.2.1). Distraction is an interesting concept in Flow research because we want to design challenges that induce high levels of Flow, but difficulty rousing participants from this state will help to confirm its presence. Hermann et al. (2015) have already developed an auditory distraction paradigm for great apes, but for comparative purposes, experimental distractions used on humans in Flow may be used in great apes. A secondary task can be introduced in a computer challenge paradigm, such as asking the participant to press a button each time they see a visual cue on the screen (e.g., Huskey et al., 2018). Alternatively, we could measure a participants’ shift in focus (if at all) towards new visual cues (Cutting & Cairns, 2020), or their ear or head

movements towards external auditory cues (Brockmyer et al., 2009). The ability to experimentally control distractions in a laboratory setting, more so than in unpredictable wild or zoo settings, further supports my recommendation for research under highly controlled conditions.

It will be particularly challenging to measure the subtractive components of the Focus dimension, i.e., a loss of self and time, in great apes. However, it is worth remembering that the subtractive components of Flow have often been criticized in human research (Jackson & Marsh 1996; Nakamura & Roberts, 2016; Ullén et al., 2012) so this is not a deal-breaker. We may be able to examine whether a great ape shows social awareness during the Flow condition (hypothesizing that in Flow, this awareness disappears). However, awareness of conspecifics overlaps with a general awareness of the outside world and it may be difficult to reliably record what a participant has lost awareness of, beyond ‘everything but the challenge at hand’.

The passage of time is a complex and continually debated topic (Gruber et al., 2015) and something we may only be able to conservatively broach in comparative Flow research. In humans, a sense of losing time during Flow is self-reported but this is not possible for animals. I suggest that great apes living with very time-regimented husbandry routines (e.g., in laboratories) could offer insights into the loss of time component of Flow. We can aim to investigate whether the expectation of timed husbandry events is impacted by being in Flow. For example, great apes can anticipate future events (Osvath & Martin-Ordas, 2014) so may ‘forget’ to show anticipatory feeding behavior if being in Flow overlaps with scheduled feeding times. Or, it may be possible to pre-train great apes to discriminate the passage of different time intervals (2 min, vs 20 min etc.), then ‘ask’ them to report how much time has elapsed following a Flow condition, versus baseline, boredom, and overload conditions.

## 6.5 Overall Flow Evaluation

In humans, Flow has been evaluated in terms of presence (Flow present vs absent) and strength (Flow on a continuum). There is currently no gold standard for evaluating Flow in humans, leading to a number of different approaches and opinions (Peifer et al., 2022).

From a comparative standpoint, finding the mere presence or absence of Flow in other species is our main objective. This requires cross-checking any animal measurements against the new comparative dimensional framework of Flow (Section 3.1). If we do not detect all six experiential components in animals, and/or they vary considerably from humans, can nonhuman Flow still be claimed? Flow has been self-reported in humans without participants meeting all classic components (Arzate & Ramirez, 2017; Csikszentmihalyi, 1990; Frochot et al., 2017), and we need to take this variation into account when considering other species.

As stated earlier, a conservative assumption is that the full, classic human Flow state will not be recognized in great apes and instead we should expect some components to be missing or weaker than others (Jackson & Marsh, 1996). As a starting point to claim the existence of Flow, I propose an animal must demonstrate components from all three dimensions (i.e., Focus, Motivation, and Affect). Weighting various components would be the next step if animal measurements met this criterion. I propose the primary components of Focus are conditional whereas the secondary components are not conditional (i.e., favorable but not mandatory). As a theoretical example, a chimpanzee sample may score highly across all dimensions, except the time component of the Focus dimension. We may therefore decide to give time-loss a lower weighting.

If an animal cannot demonstrate components from all three dimensions, there are three ways to interpret this. First Flow may truly not exist, second the conditions for Flow may not have been met (Table 1), or third there could be an alternative to Flow state (Section 6.6). Using an experimental paradigm with boredom and overload conditions (Section 3.2.3), and cross-referencing human Flow models (Figure 1) will help us deduce whether experimental conditions were met. In our theoretical example, let us imagine we found no evidence for time-loss in chimpanzees. Was this because the challenge design or experimental conditions were inadequate to induce Flow (in which case other components may also be missing), the experiment to assess time-loss was inadequate, or because time-loss did not form part of the chimpanzee

Flow experience? In animal research, it is important to be transparent about what we cannot confidently induce (i.e., Flow), or measure (cognitive skills, physiological responses, emotions, and so on), *versus* what we do not believe is present (Shettleworth, 2010).

The human Flow State Scale (Jackson & Marsh, 1996) operationalizes Flow by transforming the nine classic components (Table 1) into dimensions that load equally on a composite score (Jackson & Ecklund, 2004). The strength of Flow can therefore be measured on a continuum. A similar composite score for animals would prove useful if we first demonstrated the existence of Flow, so this would be a far later step.

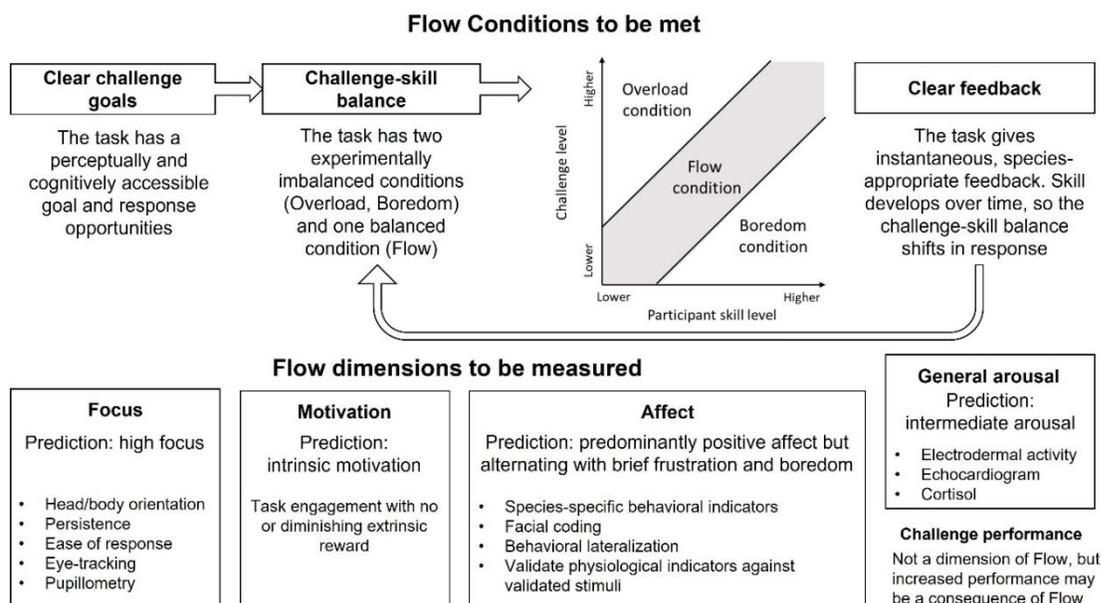
## 6.6 Alternatives to Flow State

If there is insufficient evidence for Flow in great apes, we might instead propose an alternate ‘Flow-like state’. This is supported by the close proximity of Flow to other high-focus states like anxiety (Figure 1: Asakawa, 2010; Eysenck et al., 1992; Ullén et al., 2012), and human participants being able to score highly on one Flow component without being in Flow. For example, having high focus and being objectively challenged during both an exam and a Flow activity, but these differ in terms of self- and time-awareness (Moneta, 2012). In humans, states objectively similar to Flow include high challenge engagement (synonymous with task involvement in the human literature) which scores highly on some Focus components but not others; and immersion, which is considered to be more passive than Flow (Michailidis et al., 2018).

Figure 2 summarizes the proposal to study Flow comparatively in great apes and humans using a computerized challenge paradigm. It is also applicable for future research on other taxonomic outgroups in due course.

**Figure 2**

*The Comparative Study of Flow in Great Apes and Humans in a Computerized Challenge Paradigm*



## 7 Implications of Flow in Great Apes

### 7.1 The Evolution of Happiness

The world is a difficult place to live at present, so well-being interventions are more important than ever (Alexander et al., 2021). Eudaimonia, or psychological well-being, is broadly described as the ability to find happiness in personal growth and development (Jayawickreme et al., 2012; Ryff, 2017) and it has frequently been linked to Flow (Alexander et al., 2021; Bonaiuto et al., 2016). Being able to find an internal ‘do-it yourself’ form of happiness is an appealing prospect but we still have a lot to learn about how humans find happiness, internally or externally (Jayawickreme et al., 2012; Peifer & Engeser, 2021). Whether or not Flow state exists outside our own species may challenge prevailing evolutionary theories, and suggest challenge-based happiness is more deeply-rooted than thought. And, as highlighted earlier, a lack of self-reporting in animals pushes for developments in the remote measurement of Flow.

### 7.2 Animal Welfare

#### 7.2.1 Drawbacks of Flow

Overall, Flow is taken to be a positive mental state but there is a small body of research to contest this viewpoint (reviewed by Zimanyi & Schüler, 2021). Flow can also be used for destructive activities (Csikszentmihalyi & Rathunde, 1993) because it is induced by seemingly unpleasurable situations like combat, imprisonment, and antisocial behavior (Harari, 2008). This led Harari (2008) to conclude Flow is a universal competence-enhancing experience, regardless of the positivity of the challenge.

Due to the challenge-skill balance component of Flow, the challenge has to continually get harder over time to meet the improving skills of the participant (Nakamura & Csikszentmihalyi, 2009). This ratcheting effect means increased ‘doses’ of the challenge are needed to maintain Flow (Zimanyi & Schüler, 2021). Ratcheting drives very high levels of performance, but means Flow can also become addictive and therefore performed to the detriment of other positive behaviors like socializing (Zimanyi & Schüler, 2021). Therefore, in humans at least, there is a balance to strike to ensure short-term affective benefits and avoid potential long-term negative affective outcomes of Flow. This being said, Flow has recently been posited as a protective factor against burnout (chronic work stress; Aust et al., 2022).

Could animals face similar negative consequences of Flow? Behavioral addiction has received limited study in animals compared with chemical (i.e., drug) addiction (Everitt et al., 2018), but as discussed in Section 2, primates have become addicted to laboratory tasks (Markowitz & Line, 1989; Washburn & Rumbaugh, 1992) and gambling addiction has been induced in laboratory rodents and primates (Clark et al., 2013). Another interesting welfare avenue to explore is the link between Flow and stereotypical behavior. There does not appear to be a connection between stereotyped movement and Flow in humans (Peifer & Engeser, 2021), but they arguably share some similarities within the Focus dimension, degree of coping with challenge, and behavioral compulsion (Ferdowsian et al., 2011). In a computerized Flow challenge, there is likely a fine balance to be struck between functional repetitive behavior, i.e., to learn and execute a technical skill with finger presses, and repetitive behavior which becomes stereotyped and pathological (Fam et al., 2012). Stereotypical behaviors are the most common psychopathy reported in great apes whereas other spontaneous obsessive compulsions are not apparent in the literature (Brüne et al. 2006; Fabrega 2006).

#### 7.2.2 Flow and Welfare Enhancement

The motivation to find practical welfare applications of Flow is laudable, but this should not be rushed. Once we have a better understanding of whether Flow or a Flow-like state could even be present in other species, we can work effectively towards shaping challenges to induce it. If we want to practically induce Flow to enhance animal welfare, a modified operational definition of ‘welfare-friendly’ Flow may

be needed to prevent addiction or stereotypical behaviors. Animal welfare scientists will be interested in maximizing the positive Affect dimension of Flow state, and less concerned with Focus. Since repetitive actions are diagnosed as stereotypies when they interfere with normal daily activities and self-injury (Fam et al., 2012), any observation of new stereotyped behavior in a Flow study should be grounds for terminating that challenge.

While cognitive enrichment is an increasingly popular subset of enrichment and already cited in proposals of Flow (Clark, 2017, 2022), it has been difficult to disassociate challenge participation from external food reward (Clark et al., 2019; Matrai et al., 2022; Schmelz et al., 2021). Researchers will need to incorporate more intrinsic rewards into cognitive enrichment designs, and investigate how the *process* of being challenged, not just the final outcome (e.g., Hagen & Broom, 2004; McGowan et al., 2014), impacts welfare. If Flow can be recognized using the aforementioned computerized challenge paradigm (Section 3.2.5), we might seek to modify these challenges slightly for more practical enrichment use. That being said, computerized systems are not always practical for farm, zoo, and sanctuary settings (Garcia-Pelegrin et al., 2022). A number of alternative challenges could be explored, including non-digital and social challenges which would tap into other areas of human Flow literature.

### 7.2.3 Ethics of Animal Flow Research

I was hesitant to place ethics towards the end of this paper, because it should not be viewed as a final, trivial point. For animal welfare researchers it is the most important consideration for Flow research and should be taken seriously by positive psychologists as well. What animals should be used for Flow research, and why? We must make sure the benefits outweigh the costs. If done well (i.e., through the collaboration of interdisciplinary experts), the implications of finding Flow in animals can be used to ensure better welfare conditions for many thousands of animals in captivity (Section 7.2.2). I have built a strong case for using neurophysical measures of Flow (Section 5.3) but assessing these will only be possible under highly-controlled conditions and therefore on animals living in highly unnatural environments, often wearing sensors or being in restricted spaces. To find Flow, we will likely also find boredom or anxiety/frustration in animal participants (Section 1.1) and must ensure these periods of negative affect are brief, transient, and ultimately overcome (Meehan & Mench, 2007).

## 8. Future Priorities for Comparative Flow Research

There are some promising signs, some anecdotal and some empirical, that Flow or a Flow-like state could exist in great apes. Given that great apes also find enjoyment in exploring and problem-solving, the biggest difficulty for researchers will be deciding where to draw a line in the sand between uniquely human Flow and animal Flow (or a Flow-like phenomenon). This is particularly difficult given that human Flow is variable, and a number of similar alternative states exist. Rather than these findings eroding the comparative study of Flow (*if there are so many loopholes in the definition of Flow, we will never be able to recognize it in other species*), I believe that Flow simply mirrors other complex phenomena such as social learning, culture, and intelligence. By testing the parameters of Flow in other species, we will gain a far better understanding of what Flow actually is.

For simplicity, I referred to (nonhuman) great apes as one comparative phylogenetic group in this paper. But if Flow exists, what variation might we expect to see within and across the great ape lineage? Humans with autotelic personality and ‘meta-skills’ such as general curiosity about the world, persistence, and low self-centeredness are more likely to experience Flow (Csikszentmihalyi, 1997a). In comparison, there appears to be no species-level distinction of holistic autotelic nature in great apes, although there are many studies comparing the personality traits, levels of exploration, and problem-solving between great ape species (e.g., Manrique et al., 2013; Rosati & Hare, 2013; Völter & Call, 2012).

I have proposed initial research in great apes, but research can, in due course, extend to taxonomic outgroups. These could be phylogenetically distant species with similarly developed cognitive and emotional skills (i.e., through convergent evolution) such as the bottlenose dolphin (*Tursiops truncatus*)

and *Corvidae* birds, and phylogenetically closer species with potentially less developed cognition and emotion such as *Callitrichidae* primates.

## 9. Conclusions

- Flow is a fascinating mental state currently thought to be unique to humans. However, comparative studies have not yet been undertaken. Flow is both additive (adding focus and control) and subtractive (removing a sense of time and self). The componential nature of Flow lends itself to comparative study in animals, and human research suggests it is not necessary for all components to be met to reach Flow.
- A new, three-dimensional framework of Flow that places higher importance on focus and affective state can be used to recognize Flow in great apes. The most logical approach is to experimentally induce Flow (and two adjacent conditions, boredom and overload), using a computerized challenge paradigm.
- A combination of behavioral and physiological measures is recommended for comparative research. Some measures of focus, motivation and affect have been well-validated for both humans and animals, but more research is needed to gain more confidence in the assessment of what high focus looks like in great apes.
- This paper hopes to stimulate lively debate surrounding the possibility for, and implications of, nonhuman Flow, and forge a path of collaborative research.

## Acknowledgements

Christopher Wathes and Stan Kuczaj helped to cultivate early ideas on animal Flow, further refined with the help of Georgia Mason and Joy Mench. Sincere thanks go to Iain Gilchrist, Sarah Jelbert, Bruce Hood, Michael Mendl, and Kirsten Cater at the University of Bristol for their support in developing these ideas. I would also like to thank two anonymous reviewers.

**Funding:** None

**Conflict of Interest:** The author declares no conflict of interest.

## References

- Abuhamdeh, S. (2020). Investigating the “flow” experience: Key conceptual and operational issues. *Frontiers in Psychology*, 158. doi: 10.3389/fpsyg.2020.00158
- Abuhamdeh, S. (2021). On the relationship between flow and enjoyment. In: C. Peifer & S. Engeser, S. (Eds.). *Advances in Flow Research*. Springer, New York. pp. 142–170.
- Addressi, A. R., Ferrari, L., & Carugati, F. (2015). The Flow Grid: A technique for observing and measuring emotional state in children interacting with a flow machine. *Journal of New Music Research*, 44(2), 129–144.
- Alameda, C., Sanabria, D., & Ciria, L. F. (2022). The brain in flow: a systematic review on the neural basis of the flow state. *Cortex*, 154, 348–364.
- Alexander, R., Aragón, O. R., Bookwala, J., Cherbuin, N., Gatt, J. M., Kahrilas, I. J., ... & Styliadis, C. (2021). The neuroscience of positive emotions and affect: Implications for cultivating happiness and wellbeing. *Neuroscience & Biobehavioral Reviews*, 121, 220–249.
- Altschul, D. M., Wallace, E. K., Sonnweber, R., Tomonaga, M., & Weiss, A. (2017). Chimpanzee intellect: personality, performance and motivation with touchscreen tasks. *Royal Society Open Science*, 4(5), 170169. doi: 10.1098/rsos.170169
- Amiez, C., Procyk, E., Honoré, J., Sequeira, H., & Joseph, J. P. (2003). Reward anticipation, cognition, and electrodermal activity in the conditioned monkey. *Experimental Brain Research*, 149(3), 267–275.
- Arzate, C., and Ramirez, J. A. U. (2017). Player-centered game AI from a flow perspective: towards a better understanding of past trends and future directions. *Entertainment Computing*, 20, 11–24.
- Asakawa, K. (2010). Flow experience, culture, and well-being: How do autotelic Japanese college students feel, behave, and think in their daily lives?. *Journal of Happiness Studies*, 11(2), 205–223.

- Aust, F., Beneke, T., Peifer, C., & Wekenborg, M. (2022). The Relationship between Flow Experience and Burnout Symptoms: A Systematic Review. *International Journal of Environmental Research and Public Health*, *19*(7), 3865.
- Bailey, B. P., & Iqbal, S. T. (2008). Understanding changes in mental workload during execution of goal-directed tasks and its application for interruption management. *ACM Transactions on Computer-Human Interaction (TOCHI)*, *14*(4), 1–28.
- Baumann, N. (2021). Autotelic personality. In: C. Peifer & S. Engeser, S. (Eds.). *Advances in Flow Research*. New York: Springer. Springer, New York. pp. 231–261.
- Baumann, N., & Scheffer, D. (2010). Seeing and mastering difficulty: The role of affective change in achievement flow. *Cognition and Emotion*, *24*(8), 1304–1328.
- Behringer, V., Stevens, J. M., & Sonnweber, R. (2022). Salivary Cortisol Reaction Norms in Zoo-Housed Great Apes: Diurnal Slopes and Intercepts as Indicators of Stress Response Quality. *Animals*, *12*(4), 522.
- Behringer, V., Stevens, J. M., Hohmann, G., Möstl, E., Selzer, D., & Deschner, T. (2014). Testing the effect of medical positive reinforcement training on salivary cortisol levels in bonobos and orangutans. *PLoS One*, *9*(9), e108664. doi: 10.1371/journal.pone.0108664
- Beran, M. J., Perdue, B. M., Futch, S. E., Smith, J. D., Evans, T. A., & Parrish, A. E. (2015). Go when you know: Chimpanzees' confidence movements reflect their responses in a computerized memory task. *Cognition*, *142*, 236–246.
- Beran, M. J., Savage-Rumbaugh, E. S., Pate, J. L., & Rumbaugh, D. M. (1999). Delay of gratification in chimpanzees (*Pan troglodytes*). *Developmental Psychobiology: The Journal of the International Society for Developmental Psychobiology*, *34*(2), 119–127.
- Beran, M. J., & Evans, T. A. (2006). Maintenance of delay of gratification by four chimpanzees (*Pan troglodytes*): The effects of delayed reward visibility, experimenter presence, and extended delay intervals. *Behavioural Processes*, *73*(3), 315–324.
- Berntson, G. G., & Boysen, S. T. (1989). Specificity of the cardiac response to conspecific vocalizations in chimpanzees. *Behavioral Neuroscience*, *103*(2), 235–245.
- Birkett, L. P., & Newton-Fisher, N. E. (2011). How abnormal is the behaviour of captive, zoo-living chimpanzees?. *PLoS one*, *6*(6), e21011. doi: 10.1371/journal.pone.0021011
- Bliss-Moreau, E., & Rudebeck, P. H. (2021). Animal models of human mood. *Neuroscience and Biobehavioral Reviews*, *120*, 574–582.
- Bonaiuto, M., Mao, Y., Roberts, S., Psalti, A., Ariccio, S., Ganucci Cancellieri, U., & Csikszentmihalyi, M. (2016). Optimal experience and personal growth: Flow and the consolidation of place identity. *Frontiers in Psychology*, *7*, 1654. doi: 10.3389/fpsyg.2016.01654
- Borderie, J., & Michinov, N. (2016). Identifying flow in video games: towards a new observation-based method. *International Journal of Gaming and Computer-Mediated Simulations (IJGCMS)*, *8*(3), 19–38.
- Boysen, S. T., & Berntson, G. G. (1986). Cardiac correlates of individual recognition in the chimpanzee (*Pan troglodytes*). *Journal of Comparative Psychology*, *100*(3), 321–324.
- Bräuer, J., Call, J., & Tomasello, M. (2006). Are apes really inequity averse?. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1605), 3123–3128.
- Bräuer, J., Hanus, D., Pika, S., Gray, R., & Uomini, N. (2020). Old and new approaches to animal cognition: there is not “one cognition”. *Journal of Intelligence*, *8*(3), 28.
- Brent, L., & Stone, A. M. (1996) Long-term use of televisions, balls, and mirrors as enrichment for paired and singly caged chimpanzees. *American Journal of Primatology*, *39*(2), 139–145.
- Brockmyer, J. H., Fox, C. M., Curtiss, K. A., McBroom, E., Burkhart, K. M., & Pidruzny, J. N. (2009). The development of the Game Engagement Questionnaire: A measure of engagement in video game-playing. *Journal of Experimental Social Psychology*, *45*(4), 624–634.
- Brosnan, S. F., Talbot, C., Ahlgren, M., Lambeth, S. P., & Schapiro, S. J. (2010). Mechanisms underlying responses to inequitable outcomes in chimpanzees, *Pan troglodytes*. *Animal Behaviour*, *79*(6), 1229–1237.
- Browning, H. (2020). The natural behavior debate: Two conceptions of animal welfare. *Journal of Applied Animal Welfare Science*, *23*(3), 325–337.
- Burn, C. C. (2017). Bestial boredom: A biological perspective on animal boredom and suggestions for its scientific investigation. *Animal Behaviour*, *130*, 141–151.
- Cairns, P., Cox, A., & Nordin, A. I. (2014). Immersion in digital games: review of gaming experience research. *Handbook of Digital Games*, 339, 784.
- Cheng, W. K. R. (2014). *Relationship between visual attention and flow experience in a serious educational game: An eye tracking analysis* (Doctoral dissertation, George Mason University).

- Chotard, H., Ioannou, S., & Davila-Ross, M. (2018). Infrared thermal imaging: Positive and negative emotions modify the skin temperatures of monkey and ape faces. *American Journal of Primatology*, *80*(5), e22863. doi: 10.1002/ajp.22863
- Clark, F. E. (2011). Great ape cognition and captive care: Can cognitive challenges enhance well-being?. *Applied Animal Behaviour Science*, *135*(1-2), 1–12.
- Clark, L., Averbeck, B., Payer, D., Sescousse, G., Winstanley, C. A., & Xue, G. (2013). Pathological choice: the neuroscience of gambling and gambling addiction. *Journal of Neuroscience*, *33*(45), 17617–17623.
- Clark, F. E. (2017). Cognitive enrichment and welfare: Current approaches and future directions. *Animal Behavior and Cognition* *4*(1), 52–71.
- Clark, F. E. (2022). Bridging pure cognitive research and cognitive enrichment. *Animal Cognition*, *25*, 1671-1678.
- Clark, F. E., & Smith, L. J. (2013). Effect of a cognitive challenge device containing food and non-food rewards on chimpanzee well-being. *American Journal of Primatology*, *75*(8), 807–816.
- Clark, F. E., Gray, S. I., Bennett, P., Mason, L. J., & Burgess, K. V. (2019). High-tech and tactile: Cognitive enrichment for zoo-housed gorillas. *Frontiers in Psychology*, *10*, 1574. doi:10.3389/fpsyg.2019.01574
- Csikszentmihalyi, M. (1975). *Beyond Boredom and Anxiety: Experiencing Flow in Work and Play*. Jossey Bass, San Francisco.
- Csikszentmihalyi, M. (1990). *Flow: The Psychology of Optimal Experience*. Harper & Row, New York.
- Csikszentmihalyi, M. (1997a) Finding Flow. Basic Books, New York.
- Csikszentmihalyi, M. (1997b) Evolution and Flow. *NAMTA Journal*, *22*(1), 118–49.
- Csikszentmihalyi, M. (1999). If we are so rich, why aren't we happy?. *American Psychologist*, *54*(10), 821.
- Csikszentmihalyi, M., & Rathunde, K. (1993). The measurement of flow in everyday life: toward a theory of emergent motivation. In J. E. Jacobs (Ed.), *Nebraska Symposium on Motivation, 1992: Developmental perspectives on motivation* University of Nebraska Press, Nebraska. pp. 57–97.
- Csikszentmihalyi M., Abuhamdeh S., & Nakamura J. (2005). Flow. In: Elliot A. J., Dweck C. S. Eds.). *Handbook of Competence and Motivation*. Guilford Press, New York. pp. 598–608.
- Csikszentmihalyi, M., & Larson, R. (2014). *Flow and the Foundations of Positive Psychology*, Vol. 10. Springer, Dordrecht.
- Csikszentmihalyi, M., & Nakamura, J. (1989). The dynamics of intrinsic motivation: A study of adolescents. In: C. Ames & R. Ames (Eds.). *Research on motivation in education*, Volume 3: Goals and Cognitions. Academic Press, San Diego. pp. 45–72.
- Csikszentmihalyi, M., & Nakamura, J. (2018). Flow, altered states of consciousness, and human evolution. *Journal of Consciousness Studies*, *25*(11-12), 102–114.
- Csikszentmihalyi, M., & Csikszentmihalyi, I. S. (1998). *Optimal Experience: Psychological Studies of Flow in Consciousness*. Cambridge University Press, New York.
- Custodero, L. A. (1998). Observing flow in young children's music learning. *General Music Today*, *12*(1), 21– 27.
- Cutting, J., & Cairns, P. (2020). Investigating game attention using the distraction recognition paradigm. *Behaviour & Information Technology*, 1–21.
- Dawson, M. E., Schell, A. M., & Fillion, D. L. (2007). The electrodermal system. In: J. T. Cacioppo, L. G. Tassinary L. & G. G. Berntson (Eds). *Oxford Handbook of psychophysiology*. Cambridge University Press, Cambridge. pp. 200–223.
- de Manzano, Ö., Theorell, T., Harmat, L., & Ullén, F. (2010). The psychophysiology of flow during piano playing. *Emotion*, *10*(3), 301–311.
- de Manzano, Ö., Cervenka, S., Jucaite, A., Hellenäs, O., Farde, L., & Ullén, F. (2013). Individual differences in the proneness to have flow experiences are linked to dopamine D2-receptor availability in the dorsal striatum. *Neuroimage* *67*, 1–6.
- Deci, E. L., Koestner, R., & Ryan, R. M. (1999). A meta-analytic review of experiments examining the effects of extrinsic rewards on intrinsic motivation. *Psychological Bulletin*, *125*(6), 627.
- Deci, E. L. (1975). The Intrinsic Motivation of Behavior. In E.L. Deci (Ed.). *Intrinsic Motivation*. Springer, Boston. pp. 93–125.
- Di Domenico, S. I., & Ryan, R. M. (2017). The emerging neuroscience of intrinsic motivation: A new frontier in self-determination research. *Frontiers in Human Neuroscience*, *11*, 145. doi: 10.3389/fnhum.2017.00145
- Dietrich, A. (2003) Functional neuroanatomy of altered states of consciousness: The transient hypofrontality hypothesis, *Consciousness and Cognition*, *12*, 231–256.
- Dietrich, A. (2004). Neurocognitive mechanisms underlying the experience of flow. *Conscious Cognition*, *13*, 746–761.

- Ebel, S. J., & Call, J. (2018). The interplay of prior experience and motivation in great ape problem-solving (*Gorilla gorilla*, *Pan paniscus*, *Pan troglodytes*, and *Pongo abelii*). *Journal of Comparative Psychology*, 132(3), 294.
- Egelkamp, C. L., & Ross, S. R. (2019). A review of zoo-based cognitive research using touchscreen interfaces. *Zoo Biology*, 38(2), 220–235.
- EFRN (2014). What is Flow - Current Definition. Available online at: <https://efrn.eu> (accessed November 3, 2022).
- Elder, C. M., & Menzel, C. R. (2001). Dissociation of cortisol and behavioral indicators of stress in an orangutan (*Pongo pygmaeus*) during a computerized task. *Primates*, 42(4), 345–357.
- Engeser, S., Schiepe-Tiska, A., & Peifer, C. (2021). Historical lines and an overview of current research on flow. In: C. Peifer & S. Engeser, S. (Eds.). *Advances in Flow Research*. Springer, New York. pp. 1–22.
- Eysenck, M. W., & Calvo, M. G. (1992). Anxiety and performance: The processing efficiency theory. *Cognition and Emotion*, 6(6), 409–434.
- Fagot, J., & Paleressompouille, D. (2009). Automatic testing of cognitive performance in baboons maintained in social groups. *Behavior Research Methods*, 41(2), 396–404.
- Fam, S. D., Tan, Y. S., & Waitt, C. (2012). Stereotypies in captive primates and the use of inositol: lessons from obsessive–compulsive disorder in humans. *International Journal of Primatology*, 33(4), 830–844.
- Farrar, B. G., Voudouris, K., & Clayton, N. S. (2021). Replications, comparisons, sampling and the problem of representativeness in animal cognition research. *Animal Behavior and Cognition*, 8(2), 273.
- Ferdowsian, H. R., Durham, D. L., Kimwele, C., Kranendonk, G., Otali, E., Akugizibwe, T., ... & Johnson, C. M. (2011). Signs of mood and anxiety disorders in chimpanzees. *PloS one*, 6(6), e19855. doi: 10.1371/journal.pone.0019855
- Fernández-Carriba, S., Loeches, Á., Morcillo, A., & Hopkins, W. D. (2002). Asymmetry in facial expression of emotions by chimpanzees. *Neuropsychologia*, 40(9), 1523–1533.
- Foster, M. W., Gilby, I. C., Murray, C. M., Johnson, A., Wroblewski, E. E., & Pusey, A. E. (2009). Alpha male chimpanzee grooming patterns: implications for dominance “style”. *American Journal of Primatology*, 71(2), 136– 144.
- Garcia-Pelegrin, E., Clark, F., & Miller, R. (2022). Increasing animal cognition research in zoos. *Zoo Biology*. doi: 10.1002/zoo.21674
- Gold, J., & Ciorciari, J. (2020). A Review on the Role of the Neuroscience of Flow States in the Modern World. *Behavioral Sciences*, 10(9), 137. doi: 10.3390/bs10090137
- Gruber, R. P., Bach, M., & Block, R. A. (2015). Perceiving two levels of the flow of time. *Journal of Consciousness Studies*, 22(5-6), 7–22.
- Hagen, K., & Broom, D. M. (2004). Emotional reactions to learning in cattle. *Applied Animal Behaviour Science*, 85(3-4), 203–213.
- Harari, Y. N. (2008). Combat flow: Military, political, and ethical dimensions of subjective well-being in war. *Review of General Psychology*, 12(3), 253–264.
- Harmat, L., de Manzano, Ö, Theorell, T., Högman, L., Fischer, H., & Ullén, F. (2015). Physiological correlates of the flow experience during computer game playing. *International Journal of Psychophysiology*, 97, 1–7.
- Harris, D. J., Allen, K. L., Vine, S. J., & Wilson, M. R. (2021). A systematic review and meta-analysis of the relationship between flow states and performance. *International Review of Sport and Exercise Psychology*. doi: 10.1080/1750984X.2021.1929402
- Harris, D. J., Vine, S. J., & Wilson, M. R. (2019). An external focus of attention promotes flow experience during simulated driving. *European Journal of Sport Science*, 19(6), 824–833.
- Harris, D. J., Vine, S. J., & Wilson, M. R. (2017a). Neurocognitive mechanisms of the flow state. *Progress in Brain Research*. 234, 221–243.
- Harris, D. J., Vine, S. J., & Wilson, M. R. (2017b). Is flow really effortless? The complex role of effortful attention. *Sport, Exercise, and Performance Psychology*, 6, 103. doi: 10.1037/spy0000083
- Harris, D. J., Vine, S. J., & Wilson, M. R. (2017c). Flow and quiet eye: the role of attentional control in flow experience. *Cognitive Processes*, 18, 343–347.
- Healy, S. D. (2021). The Technical Brain. In: Healy, S.D. *Adaptation and the Brain*. Oxford University Press, Oxford. pp.67-80.
- Hektner, J. M., Schmidt, J. A., & Csikszentmihalyi, M. (2007). *Experience Sampling Method: Measuring the Quality of Everyday Life*. Sage Publications, California.
- Hepach, R., Vaish, A., Kano, F., Albiach-Serrano, A., Benziad, L., Call, J., & Tomasello, M. (2020). Chimpanzees’ (*Pan troglodytes*) internal arousal remains elevated if they cannot themselves help a conspecific. *Journal of Comparative Psychology*, 135(2): 196–207.

- Hintze, S., & Yee, J. R. (2021). Animals in flow—Towards the scientific study of intrinsic reward in animals. <https://psyarxiv.com/h6aw3/>
- Hirata, S., Matsuda, G., Ueno, A., Fukushima, H., Fuwa, K., Sugama, K., ... & Hasegawa, T. (2013). Brain response to affective pictures in the chimpanzee. *Scientific reports*, 3(1), 1–5.
- Hopper, L. M., Gulli, R. A., Howard, L. H., Kano, F., Krupenye, C., Ryan, A. M., & Paukner, A. (2021). The application of noninvasive, restraint-free eye-tracking methods for use with nonhuman primates. *Behavior Research Methods*, 53(3), 1003–1030.
- Huskey, R., Wilcox, S., & Weber, R. (2018). Network neuroscience reveals distinct neuromarkers of flow during media use. *Journal of Communication* 68, 872–895.
- Inal, Y., & Cagiltay, K. (2007). Flow experiences of children in an interactive social game environment. *British Journal of Educational Technology*, 38(3), 455–464.
- Itakura, S. (1993). Emotional behavior during the learning of a contingency task in a chimpanzee. *Perceptual and Motor Skills*, 76(2), 563–566.
- Jackson, S. A., & Csikszentmihalyi, M. (1999). *Flow in Sports: The keys to optimal experiences and performances*. Human Kinetics, Illinois.
- Jackson, S. A., and Marsh, H. (1996). Development and validation of a scale to measure optimal experience: the flow state scale. *Journal of Sport and Exercise Psychology* 18, 17–35.
- Jackson, S. A., & Eklund, R. C. (2004). *The Flow Scales Manual*. Fitness Information Technology. Morgantown, West Virginia.
- Jayawickreme, E., Forgeard, M. J., & Seligman, M. E. (2012). The engine of well-being. *Review of General Psychology*, 16(4), 327–342.
- Kaneko, T., & Tomonaga, M. (2011). The perception of self-agency in chimpanzees (Pan troglodytes). *Proceedings of the Royal Society B: Biological Sciences*, 278(1725), 3694–3702.
- Kangas, B. D., & Bergman, J. (2017). Touchscreen technology in the study of cognition-related behavior. *Behavioural Pharmacology*, 28(8), 623.
- Kano, F., & Tomonaga, M. (2009). How chimpanzees look at pictures: a comparative eye-tracking study. *Proceedings of the Royal Society B: Biological Sciences*, 276(1664), 1949–1955.
- Kano, F., & Tomonaga, M. (2013). Head-mounted eye tracking of a chimpanzee under naturalistic conditions. *PLoS one*, 8(3), e59785. doi: 10.1371/journal.pone.0059785
- Kano, F., Hirata, S., Deschner, T., Behringer, V., & Call, J. (2016). Nasal temperature drop in response to a playback of conspecific fights in chimpanzees: A thermo-imaging study. *Physiology and Behavior*, 155, 83–94.
- Kawabata, M., & Mallett, C. J. (2011). Flow experience in physical activity: Examination of the internal structure of flow from a process-related perspective. *Motivation and Emotion*, 35(4), 393–402.
- Kaye, L. K., Monk, R. L., Wall, H. J., Hamlin, I., & Qureshi, A. W. (2018). The effect of flow and context on in-vivo positive mood in digital gaming. *International Journal of Human Communication Studies*, 110, 45–52.
- Keller, J., Bless, H., Blomann, F., & Kleinböhl, D. (2011). Physiological aspects of flow experiences: Skills-demand-compatibility effects on heart rate variability and salivary cortisol. *Journal of Experimental Social Psychology*, 47, 849–852.
- Kim, J., Seo, J., & Laine, T. H. (2018). Detecting boredom from eye gaze and EEG. *Biomedical Signal Processing and Control*, 46, 302–313.
- Kivikangas, J. M. (2006). Psychophysiology of flow experience: An explorative study. (Masters dissertation, University of Helsinki).
- Klasen, M., Weber, R., Kircher, T. T., Mathiak, K. A., & Mathiak, K. (2012). Neural contributions to flow experience during video game playing. *Social Cognitive and Affective Neuroscience*. 7, 485–495.
- Ko, S. M., & Ji, Y. G. (2018). How we can measure the non-driving-task engagement in automated driving: comparing flow experience and workload. *Applied Ergonomics*, 67, 237–245.
- Kremer, L., Holkenborg, S. K., Reimert, I., Bolhuis, J. E., & Webb, L. E. (2020). The nuts and bolts of animal emotion. *Neuroscience & Biobehavioral Reviews*, 113, 273–286.
- Kret, M. E., Prochazkova, E., Sterck, E. H., & Clay, Z. (2020). Emotional expressions in human and non-human great apes. *Neuroscience & Biobehavioral Reviews*, 115, 378–395.
- Krupenye, C., & Call, J. (2019). Theory of mind in animals: Current and future directions. *Wiley Interdisciplinary Reviews: Cognitive Science*, 10(6), e1503. doi: 10.1002/wcs.1503
- Kuraoka, K., & Nakamura, K. (2022). Facial temperature and pupil size as indicators of internal state in primates. *Neuroscience Research*. doi: 10.1016/j.neures.2022.01.002

- Laine, C. M., Spitler, K. M., Mosher, C. P., & Gothard, K. M. (2009). Behavioral triggers of skin conductance responses and their neural correlates in the primate amygdala. *Journal of Neurophysiology*, *101*(4), 1749–1754.
- Langbein, J., Siebert, K., & Nürnberg, G. (2009). On the use of an automated learning device by group-housed dwarf goats: do goats seek cognitive challenges? *Applied Animal Behaviour Science*, *120*, 150–158.
- Laméris, D. W., Verspeek, J., Salas, M., Staes, N., Torfs, J. R. R., Eens, M., & Stevens, J. M. G. (2022a). Evaluating Self-Directed Behaviours and Their Association with Emotional Arousal across Two Cognitive Tasks in Bonobos (*Pan paniscus*). *Animals* *12*, 3002. doi: 10.3390/ani12213002
- Laméris, D. W., Verspeek, J., Eens, M., & Stevens, J. M. (2022b). Social and nonsocial stimuli alter the performance of bonobos during a pictorial emotional Stroop task. *American Journal of Primatology*, *84*(2), e23356. doi: 10.1002/ajp.23356
- Larsen, J. T., Berntson, G. G., Poehlmann, K. M., Ito, T. A., & Cacioppo, J. T. (2008). *The psychophysiology of emotion*. In M. Lewis, J. M. Haviland-Jones, & L. F. Barrett (Eds.). *Handbook of emotions*. The Guilford Press, London. pp. 180–195.
- Leavens, D., Hopkins, W., & Aureli, F. (2004). Behavioral evidence for the cutaneous expression of emotion in a chimpanzee (*Pan troglodytes*). *Behaviour*, *141*(8), 979–997.
- Leavens, D.A., Aureli, F., Hopkins, W.D., & Hyatt, C.W. (2001). Effects of cognitive challenge on self-directed behaviors by chimpanzees (*Pan troglodytes*). *American Journal of Primatology*. *55*, 1–14.
- MacLean, E. L. (2016). Unraveling the evolution of uniquely human cognition. *Proceedings of the National Academy of Sciences*, *113*(23), 6348–6354.
- Manrique, H. M., Völter, C. J., & Call, J. (2013). Repeated innovation in great apes. *Animal Behaviour*, *85*(1), 195–202.
- Markowitz, H., & Line, S. (1989). *Primate Research Models and Environmental Enrichment*. Noyes Publications, New Jersey.
- Marzouki, Y., Gullstrand, J., Goujon, A., & Fagot, J. (2014). Baboons' response speed is biased by their moods. *PLoS one*, *9*(7), e102562. doi: 10.1371/journal.pone.0102562
- Maslow A.H. (1970): *Motivation and Personality* (2nd ed.). Harper & Row, New York.
- Maslow A. H. (1987): *Motivation and Personality* (3rd ed., revised by R. Frager, J. Fadiman, C. McReynolds & R. Cox). Harper & Row, New York.
- Mason, G. J. (1991). Stereotypes and suffering. *Behavioural Processes*, *25*, 103–115.
- Massen, J. J., Antonides, A., Arnold, A. M. K., Bionda, T., & Koski, S. E. (2013). A behavioral view on chimpanzee personality: Exploration tendency, persistence, boldness, and tool-orientation measured with group experiments. *American Journal of Primatology*, *75*(9), 947–958.
- Matrai, E., Kwok, S. T., Boos, M., & Pogány, Á. (2022). Testing use of the first multi-partner cognitive enrichment devices by a group of male bottlenose dolphins. *Animal Cognition*, *25*, 961–973
- McGowan, R. T., Rehn, T., Norling, Y., & Keeling, L. J. (2014). Positive affect and learning: exploring the “Eureka Effect” in dogs. *Animal cognition*, *17*(3), 577–587.
- Meehan, C.L., & Mench, J.A. (2007). The challenge of challenge: can problem solving opportunities enhance animal welfare? *Applied Animal Behaviour Science*, *102*, 246–261.
- Michailidis, L., Balaguer-Ballester, E., & He, X. (2018). Flow and immersion in video games: The aftermath of a conceptual challenge. *Frontiers in Psychology*, *9*, 1682. doi: 10.3389/fpsyg.2018.01682
- Moneta, G. B. (2004). The flow experience across cultures. *Journal of Happiness Studies: An Interdisciplinary Forum on Subjective Well-Being*, *5*(2), 115–121
- Moneta, G. B. (2012). On the measurement and conceptualization of flow. In S. Engeser (Ed.). *Advances in Flow Research*. Springer, New York. pp. 23–50.
- Morimura, N. (2006). Cognitive enrichment in chimpanzees: An approach of welfare entailing an animal's entire resources. In: T. Matsuzawa, M. Tomonaga & M. Tanaka (Eds.). *Cognitive development in chimpanzees*. Springer, Tokyo. pp. 368–391.
- Nacke, L. E., Stellmach, S., & Lindley, C. A. (2010). Electroencephalographic assessment of player experience: a pilot study in affective ludology. *Simulation and Gaming* *42*, 632–655.
- Nah, F. F. H., Yelamanchili, T., and Siau, K. (2017). A review on neuropsychophysiological correlates of flow. *Proceedings of the International Conference on HCI in Business, Government, and Organizations*. 364–372.
- Nakamura, J., & Roberts, S. (2016) The hypo-egoic component of flow. In: K.W. Brown & M.R Leary (Eds.). *Oxford Handbook of Hypo-Egoic Phenomena*. Oxford University Press, New York. pp. 133–146.
- Nakamura, J., & Csikszentmihalyi, M. (2002). The concept of flow. In: C. R. Snyder & S. J. Lopez (Eds.), *Handbook of Positive Psychology*. Oxford University Press, New York. pp. 89–105.

- Nakamura, J., & Csikszentmihalyi, M. (2009). Flow theory and research. In S. J. Lopez & C. R. Snyder (Eds.). *Oxford handbook of positive psychology*, Second edition. Oxford University Press, New York. pp. 195–206.
- Nieuwburg, E. G., Ploeger, A., & Kret, M. E. (2021). Emotion recognition in nonhuman primates: how experimental research can contribute to a better understanding of underlying mechanisms. *Neuroscience & Biobehavioral Reviews*, *123*, 24–47.
- Nielsen, M., Collier-Baker, E., Davis, J. M., & Suddendorf, T. (2005). Imitation recognition in a captive chimpanzee (*Pan troglodytes*). *Animal Cognition*, *8*, 31–36.
- Norsworthy, C., Jackson, B., & Dimmock, J. A. (2021). Advancing our understanding of psychological flow: A scoping review of conceptualizations, measurements, and applications. *Psychological Bulletin*, *147*(8), 806–827.
- Novak, T. P., Hoffman, D. L., & Yung, Y.-F. (2000). Measuring the customer experience in online environments: a structural modeling approach. *Marketing Science*, *19*, 22–42.
- Novak, M. A., Hamel, A. F., Kelly, B. J., Dettmer, A. M., & Meyer, J. S. (2013). Stress, the HPA axis, and nonhuman primate well-being: A review. *Applied Animal Behaviour Science*, *143*(2–4), 135–149.
- Oh, J., Jeong, S. Y., & Jeong, J. (2012). The timing and temporal patterns of eye blinking are dynamically modulated by attention. *Human Movement Science*, *31*(6), 1353–1365.
- Osborne, S. R. (1977). The free food (contrafreeloading) phenomenon: A review and analysis. *Animal Learning & Behavior*, *5*(3), 221–235.
- Osvath, M., & Martin-Ordas, G. (2014). The future of future-oriented cognition in non-humans: theory and the empirical case of the great apes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1655), 20130486.
- Padrell, M., Amici, F., Córdoba, M. P., & Llorente, M. (2022). Cognitive enrichment in a social setting: assessing the use of a novel food maze in sanctuary-housed chimpanzees. *Primates*, *63*(5), 509–524.
- Parr, L. A. (2001). Cognitive and physiological markers of emotional awareness in chimpanzees (*Pan troglodytes*). *Animal Cognition*, *4*(3), 223–229.
- Parr, L. A., & Hopkins, W. D. (2000). Brain temperature asymmetries and emotional perception in chimpanzees, *Pan troglodytes*. *Physiology & behavior*, *71*(3–4), 363–371.
- Peifer, C., & Engeser, S. (Eds.). (2021). *Advances in Flow Research*. Springer, New York
- Peifer, C., & Tan, J. (2021). The psychophysiology of flow experience. In: C. Peifer & S. Engeser (Eds.). *Advances in Flow Research*. Springer, New York. pp. 191–230.
- Perdue, B. M., Evans, T. A., Washburn, D. A., Rumbaugh, D. M., & Beran, M. J. (2014). Do monkeys choose to choose?. *Learning and Behavior*, *42*(2), 164–175.
- Peifer, C., Wolters, G., Harmat, L., Heutte, J., Tan, J., Freire, T., ... & Triberti, S. (2022). A Scoping Review of Flow Research. *Frontiers in Psychology*, *13*, 815665. doi: 10.3389/fpsyg.2022.815665
- Phelps, E. A. (2006). Emotion and cognition: insights from studies of the human amygdala. *Annual Review of Psychology*, *57*, 27–53.
- Redelmeier, D. A., & Kahneman, D. (1996). Patients' memories of painful medical treatments: Real-time and retrospective evaluations of two minimally invasive procedures. *Pain*, *66*(1), 3–8.
- Rosati, A. G., & Hare, B. (2013). Chimpanzees and bonobos exhibit emotional responses to decision outcomes. *PloS one*, *8*(5), e63058. doi: 10.1371/journal.pone.0063058
- Rosati, A. G., Herrmann, E., Kaminski, J., Krupenye, C., Melis, A. P., Schroepfer, K., Tan, J., Warneken, F., Wobber, V., & Hare, B. (2013). Assessing the psychological health of captive and wild apes: A response to Ferdowsian et al. (2011). *Journal of Comparative Psychology*, *127*(3), 329–336.
- Ross, S. R., Lake, B. R., Fultz, A., & Hopper, L. M. (2021). An evaluation of thermal imaging as a welfare monitoring tool for captive chimpanzees. *Primates*, *62*(6), 919–927.
- Russon, A. E. (2004). Great ape cognitive systems. In: A. E. Russon & D. R. Begun (eds). *The evolution of thought: Evolutionary origins of great ape intelligence*. Cambridge University Press, Cambridge. pp. 76–100.
- Ryan, R. M., & Deci, E. L. (2001). On happiness and human potentials: A review of research on hedonic and eudaimonic well-being. *Annual Review of Psychology*, *52*(1), 141–166.
- Ryff, C. D. (2017). Eudaimonic well-being, inequality, and health: Recent findings and future directions. *International Review of Economics*, *64*(2), 159–178.
- Sanchez-Vives, M. V., & Slater, M. (2005). From presence to consciousness through virtual reality. *Nature Reviews Neuroscience* *6*:332. doi: 10.1038/nrn1651
- Sato, Y., Kitazaki, M., Itakura, S., Morita, T., Sakuraba, Y., Tomonaga, M., & Hirata, S. (2021). Great apes' understanding of biomechanics: eye-tracking experiments using three-dimensional computer-generated animations. *Primates*, *62*(5), 735–747.

- Schmelz, M., & Krause, E. T. (2021). Simple but Complex—A Laying Hen Study as Proof of Concept of a Novel Method for Cognitive Enrichment and Research. *Frontiers in Animal Science*, 2, 18. doi: 10.3389/fanim.2021.671905
- Schwarz, N., & Clore, G. L. (2003). Mood as information: 20 years later. *Psychological Inquiry*, 14, 294–301.
- Seitz, B. M., McCune, K., MacPherson, M., Bergeron, L., Blaisdell, A. P., & Logan, C. J. (2021). Using touchscreen equipped operant chambers to study animal cognition. Benefits, limitations, and advice. *PloS one*, 16(2), e0246446. doi: 10.1371/journal.pone.0246446
- Seligman, M. E. (2002). Positive psychology, positive prevention, and positive therapy. In C. Snyder, & S. Lopez (Eds.). *Handbook of positive psychology*. Oxford University Press, Oxford. pp.3-12.
- Semendeferi, K., Armstrong, E., Schleicher, A., Zilles, K., & Van Hoesen, G. W. (2001). Prefrontal cortex in humans and apes: a comparative study of area 10. *American Journal of Physical Anthropology*, 114(3), 224–241.
- Shaw, R. C., & Schmelz, M. (2017). Cognitive test batteries in animal cognition research: evaluating the past, present and future of comparative psychometrics. *Animal Cognition*, 20(6), 1003-1018.
- Shettleworth, S. J. (2010). Clever animals and killjoy explanations in comparative psychology. *Trends in Cognitive Sciences*, 14(11), 477–481.
- Sinnamon, S., Moran, A., & O’Connell, M. (2012). Flow among musicians: Measuring peak experiences of student performers. *Journal of Research in Music Education*, 60(1), 6–25.
- Swann, C., Keegan, R. J., Piggott, D., & Crust, L. (2012). A systematic review of the experience, occurrence, and controllability of flow states in elite sport. *Psychology of Sport and Exercise*, 13(6), 807-819.
- Toates, F. (2004). Cognition, motivation, emotion and action: a dynamic and vulnerable interdependence. *Applied Animal Behaviour Science*, 86(3-4), 173–204.
- Tordet, C., Erhel, S., Wodey, E., Jamet, E., Nardi, N., & Gonthier, C. (2021). The Flow Observational Grid: An observation-based solution to assess flow states. *Journal of Happiness Studies*, 22(7), 3069–3089.
- Ullén, F., de Manzano, Ö., Almeida, R., Magnusson, P. K. E., Pedersen, P. L., Nakamura, J., Csikszentmihályi, M., & Madison, G. (2012). Proneness for psychological flow in everyday life: Associations with personality and intelligence. *Personality and Individual Differences*, 52(2): 167–172.
- Ulrich, M., Keller, J., Hoenig, K., Waller, C., & Grön, G. (2014). Neural correlates of experimentally induced flow experiences. *Neuroimage* 86, 194–202.
- Unsworth, N., & Robison, M. K. (2018). Tracking arousal state and mind wandering with pupillometry. *Cognitive, Affective, & Behavioral Neuroscience*, 18(4), 638–664.
- Van der Linden, D., Tops, M., & Bakker, A. B. (2021). The Neuroscience of the Flow State: Involvement of the Locus Coeruleus Norepinephrine System. *Frontiers in Psychology*, 12: 645498. doi: 10.3389/fpsyg.2021.645498
- Vittersø, J., & Søholt, Y. (2011). Life satisfaction goes with pleasure and personal growth goes with interest: Further arguments for separating hedonic and Eudaimonic well-being. *The Journal of Positive Psychology*, 6(4), 326–335.
- Völter, C. J., & Call, J. (2012). *Problem solving in great apes (Pan paniscus, Pan troglodytes, Gorilla gorilla, and Pongo abelii)*: the effect of visual feedback. *Animal Cognition*, 15(5), 923–936.
- Völter, C. J., Reindl, E., Felsche, E., Civelek, Z., Whalen, A., Lugosi, Z., ... & Seed, A. M. (2022). The structure of executive functions in preschool children and chimpanzees. *Scientific reports*, 12(1), 1–16.
- Wagner, K. E., Hopper, L. M., & Ross, S. R. (2016). Asymmetries in the production of self-directed behavior by chimpanzees and gorillas during a computerized cognitive test. *Animal Cognition*, 19(2), 343–350.
- Walker, C. J. (2010). Experiencing flow: Is doing it together better than doing it alone?. *The Journal of Positive Psychology*, 5(1), 3–11.
- Waller, B. M., Julle-Daniere, E., & Micheletta, J. (2020). Measuring the evolution of facial ‘expression’ using multi-species FACS. *Neuroscience & Biobehavioral Reviews*, 113, 1–11.
- Waller, B. M., Misch, A., Whitehouse, J., & Herrmann, E. (2014). Children, but not chimpanzees, have facial correlates of determination. *Biology Letters*, 10(3), 20130974. doi: 10.1098/rsbl.2013.0974
- Washburn, D. A., Salamanca, J. A., Callery, R. C., & Whitham, W. (2017). Tools for measuring animal cognition: T mazes to touchscreens. In: J. Call, G. M. Burghardt, I. M. Pepperberg, C. T. Snowdon, & T. Zentall (Eds.). *APA handbook of comparative psychology: Basic concepts, methods, neural substrate, and behavior*. American Psychological Association. pp. 115–132.
- Washburn, D.A., & Rumbaugh, D.M., 1992. Testing primates with joystick-based automated apparatus: Lessons from the Language Research Center’s Computerized Test System. *Behavior Research Methods, Instruments, & Computers*, 24, 157–164.
- Waterman, A. S. (1993). Two conceptions of happiness: Contrasts of personal expressiveness (eudaimonia) and hedonic enjoyment. *Journal of Personality and Social Psychology*, 64, 678–691.

- Weber, R., Huskey, R., & Craighead, B., 2017. Flow experiences and well-being. In: L. Reinecke & M.B. Oliver (Eds.). *The Routledge Handbook of Media Use and Well-being: International Perspectives on Theory and Research on Positive Media Effects*. Routledge, London. pp. 183–196.
- Weber, R., Tamborini, R., Westcott-Baker, A., & Kantor, B. (2009). Theorizing flow and media enjoyment as cognitive synchronization of attentional and reward networks. *Communication Theory* 19, 397– 422.
- Yamanashi, Y., & Matsuzawa, T. (2010). Emotional consequences when chimpanzees (*Pan troglodytes*) face challenges: individual differences in self-directed behaviours during cognitive tasks. *Animal Welfare*, 19(1), 25–30.
- Yamanashi, Y., & Hayashi, M. (2011). Assessing the effects of cognitive experiments on the welfare of captive chimpanzees (*Pan troglodytes*) by direct comparison of activity budget between wild and captive chimpanzees. *American Journal of Primatology*, 73(12), 1231-1238.
- Yamanashi, Y., Matsunaga, M., Shimada, K., Kado, R., & Tanaka, M. (2016). Introducing tool-based feeders to zoo-housed chimpanzees as a cognitive challenge: spontaneous acquisition of new types of tool use and effects on behaviours and use of space. *Journal of Zoo and Aquarium Research*, 4(3), 147–155.
- Yamanashi, Y., Hitoosa, K., Yoshida, N., Kano, F., Ikkatai, Y., & Sakamoto, H. (2022). Do chimpanzees enjoy a virtual forest? A pilot investigation of the use of interactive art as a form of environmental enrichment for zoo-housed chimpanzees. *American Journal of Primatology*, 84(10), e23343.
- Yoshida, K., Sawamura, D., Inagaki, Y., Ogawa, K., Ikoma, K., & Sakai, S. (2014). Brain activity during the flow experience: a functional near-infrared spectroscopy study. *Neuroscience Letters* 573, 30–34.
- Young, R. J. (2013). *Environmental enrichment for captive animals*. London, John Wiley & Sons.
- Zimanyi, Z., & Schüler, J. The dark side of the moon. In: C. Peifer & S. Engeser (Eds.). *Advances in Flow Research*. Springer, New York. pp. 171–190.