

Temporal Cognition in Apes

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In humans, at least some of our ability to coordinate our actions with the timing of events in our world is due to our capacities for temporal cognition. However, controversy arises when we turn our attention to the animal world. In this paper, we will argue that apes, especially Tai Chimpanzees, are capable of genuine temporal cognition. That is, they are able to mentally represent and reason about time in cognition. We do this by developing a novel analysis of the mental representation of time.

Keywords: temporal cognition, animal cognition, temporal representation, cognitive science

1 Introduction

Across the living world, organisms must coordinate their activities with the timing of events around them. This *temporal coordination* occurs at a range of timescales – from behaviours expressed over the course of the lifespan, years, months, days, hours, minutes, to milliseconds. In humans, at least some of our ability to coordinate our actions with the timing of events in our world is the result of temporal cognition. We often reason and think about time, and the timing of events, in order to guide our behaviours.

However, controversy arises when we turn to the animal world. For some (e.g., Boroditsky and Prinz, 2008), temporal cognition requires linguistic competencies that endow creatures with the ability to mentally represent time. For others, temporal cognition requires the capacity for causal reasoning which is only found in competent humans (Hoerl and McCormack, 2018). For others still, temporal cognition requires the capacity for episodic memory, which is arguably missing in non-human animals (see discussions in Clayton, Russel, and Dickinson 2009; Suddendorf and Corballis, 2007; Roberts, 2002; Tulving 1985). According to these deflationary positions, temporal coordination in animals is not brought about through temporal cognition, or even any capacity for temporal representation, but rather through a mere temporal sensitivity to time-dependent processes (see section 2 for an explication of this notion of temporal sensitivity).

In this paper, we will argue that apes, especially Tai Chimpanzees, are capable of genuine temporal cognition. That is, they are able to mentally represent and reason about time in cognition.

Section 2 clarifies the debate by distinguishing between explanations of temporal coordination which employ temporal cognition from those that employ mere temporal sensitivities.

Section 3 explains how empirical evidence can be used to distinguish between these distinct cognitive architectures. We argue that cognitive architectures that employ general temporal representations exhibit a certain cluster of behaviours. These behaviours thereby act as epistemic markers that the animal's cognitive architecture employs representations of time and temporal properties. It is these markers that we should look for in order to find empirical evidence of temporal cognition.

Section 4 describes two case studies of Tai Chimpanzees, one involving hunting and the second foraging, in the wild which exhibit these behavioural markers. Section 5 discusses how these findings could be generalized to other apes.

We conclude by drawing out the implications of our account and how this account provides methodological tools for comparative psychology more generally.

2 Temporal Representation and Temporal Sensitivity

It is well documented that individual animals are capable of coordinating their actions with the timing of events around them across a strikingly wide range of timescales – from years through milliseconds (Buhusi & Meck 2005). The question at hand is what sort of cognitive architectures underpin these varieties of temporal coordination.

In adult humans, we know that some temporal coordination is brought about through cognitive processes that operate over explicit representations of time – that is, we rely on *temporal cognition*.¹ For instance, consider what it takes to catch a flight. To plan your journey, you must know, at a minimum, when your flight leaves, how long it takes to arrive at the airport, and that you must arrive at the airport before your flight. Then, to implement your plan, you must keep track of time to know when these events will occur in relation to the present moment. Catching a flight relies on cognitive processes like these that operate over representations of time and temporal properties. For our purposes, this sort of reasoning is our exemplar of temporal cognition.²

While it's generally agreed that adult humans can employ temporal cognition for the purposes of temporal coordination, the issue becomes less clear when we turn to the animal world.³ In order for an animal to employ temporal cognition that animal must have the capacity to mentally represent time. Yet it is this very representational capacity that has been the target of scepticism. For Hoerl & McCormack (2018), the ability to mentally represent time requires a capacity for causal reasoning, which they argue non-human animals lack. For others, such as

¹ Our use of the term 'temporal cognition' is more restrictive than some uses. For instance, what Hoerl & McCormack call *temporal updating* would not count as a form of temporal cognition by our lights, since it does not involve temporal representation.

² Temporal cognition, as described here, encompasses more than just episodic memory (Buhusi & Meck, 2005; Palombo, Keane & Verfaellie, 2016). Therefore, arguments that animals lack temporal cognition due to lacking episodic memory (e.g., Roberts 2002) are invalid.

³ Some deny that any cognitive processes are defined over mental representations (for instance Hutto & Myin 2012; 2017). Therefore, these researchers deny that even adult humans possess temporal cognition as specified here.

Boroditsky & Prinz (2008), the ability to mentally represent time requires a public language which non-human animals arguably lack. For others, (Suddendorf & Corballis, 2007; Tulving 1985; Roberts 2002; and discussion in Clayton, Russel, and Dickinson, 2009), the ability to mentally represent time requires the capacity for episodic memory, which these authors argue is uniquely human.

In all of these cases, animals are thought to lack the capacity to represent time since they lack some more foundational cognitive capacity. These authors provide deflationary explanations of temporal coordination which appeal to these animals exploiting mere sensitivities to (either internal or external) time-dependent processes. As a result, the cognitive architecture of these animals would differ drastically from our own cognitive architecture.⁴ Two examples from the literature are helpful in illustrating these contrasting cognitive architectures (both examples are found in Peacocke, 2017; 2019).

CIRCADIAN FORAGING: Animals can associate the location of food availability with specific times of day. These associations can even be formed and maintained when animals are kept in artificial conditions in which all time-of-day cues are removed. For instance, a hamster might associate the availability of food in one branch of a maze with the evening and the availability of food in another branch of the maze in the morning, despite the hamster receiving no external cues that could help them keep track of the time of day. A hamster trained in this way will exhibit anticipatory feeding behaviours by going to the expected location of food at the appropriate time of day (Mulder et al., 2013). Since the hamster cannot use external cues to keep track of time there must be something internal to them that is doing this work. It is now widely accepted that this internal mechanism is an oscillatory mechanism that cycles through a series of states approximately every 24 hours (Weaver, 1998).

One way of explaining this circadian behaviour appeals to temporal cognition. Animals possess an internal oscillator which represents the time of day, and they form a memory for when food is available at specific locations. The animal then uses these representational mechanisms to guide their behaviour.

However, a deflationary explanation of this behaviour is also available. Animals simply associate the presence of food at a certain location with a phase of a nonrepresentational internal oscillator.⁵ When the oscillator hits a certain phase, regardless of the time of day, the animal will expect food at a certain location. Temporal coordination results from the oscillator, and subsequent associated behaviours, being synchronized with the environment. The animal thereby coordinates its activities with time without the need for any temporal representation. All that is needed is that the animal's activities are sensitive to the development of a time-dependent process.⁶

AMAKIHI FORAGING: The amakihi bird of Hawaii feeds on flowers that replenish their nectar at a predictable rate. After feeding on a flower, if they return too quickly, the flower will not have replenished its nectar. Yet waiting too long gives rival foragers an opportunity to eat the nectar. Therefore, the amakihi coordinate their feeding with the time it takes the flowers to replenish

⁴ For discussion of this issue see Hoerl & McCormack (2018).

⁵ Whether the animal is conscious of this association is something that we can remain neutral on.

⁶ Hoerl and McCormack's (2018) temporal updating system would be an example of this deflationary explanation while their temporal reasoning system is a form of temporal cognition.

their nectar. This behavioural pattern has been widely observed (Gallistel, 1990) and it is this coordination that needs explanation.

The same types of explanations as we had in the circadian foraging case apply here. One explanation appeals to temporal cognition. The amakihi remembers when it fed on specific flowers, represents how long it takes for the flowers to replenish their nectar, and represents how much time has passed since its fed on specific flowers. They then perform an inference to determine their feeding behaviours.

The deflationary explanation does without representations of time. The bird simply associates the presence of food at specific flowers with the state of a time-dependent process. For instance, the bird may have some internal accumulator mechanism that simply triggers the tokening of a representation of food at a specific location after a certain amount of time has passed (Hoerl & McCormack 2018). Alternatively, the bird may associate food availability with some other time-dependent process. If, for instance, the bird feeds at a regular rate, then the bird may count how many times it has fed and only return to flowers after a certain number of feedings. In either case, no representation of time is needed. Rather, the bird coordinates its behaviours with the timing of events by exploiting associations with nonrepresentational time-dependent processes. Its activities are sensitive to time without relying on temporal cognition.

In both cases, the deflationary explanations are the same. Temporal coordination is brought about without temporal representations. Rather, temporal coordination is brought about by associating states of the world and actions with processes that unfold in (but do not represent) time. Therefore, the mere observation of temporal coordination, does not show that an animal is capable of temporal cognition.

The question we now face is how to determine whether any given animal is capable of temporal cognition. The literature contains a few proposals.

Tyler Burge (2010; 2022) has articulated a constitutive account of temporal representation by characterizing those properties a temporal sensitivity must instantiate for it to be a temporal representation.⁷ According to Burge, it is “[a] functioning psychological coordination of [the representation] of other matters with temporal sensitivity is both necessary and sufficient for temporal representation...” (Burge 2010: 521). An animal capable of mentally representing time is nothing more than an animal that possesses a temporal sensitivity that is appropriately integrated with the rest of their cognitive architecture.

If Burge is correct, then the cases described above, CIRCADIAN FORAGING and AMAKIHI FORAGING, would both turn out to involve genuine temporal cognition. Deflationary explanations of these behaviours would not be possible since these cases involve temporal sensitivities that are integrated with the representation of non-temporal matters of fact.

Importantly, not all temporal sensitivities constitute temporal representations for Burge, so some deflationary explanations of temporal coordination are possible. Consider the circadian control of sleep/wake cycles. Suppose that an oscillatory mechanism controls the production of sleep hormones and is not integrated with any other representational capacities. Given that this oscillatory mechanism is calibrated with the local day/night cycle, the resulting sleep/wake cycles would be coordinated with the local environment as a result of the oscillator leading to

⁷ Burge is concerned with distinguishing between mere temporal sensitivities and representations in perception. While he does not apply this analysis to the parallel distinction in cognition, it is this analysis of temporal representation that matters for our purposes.

regular hormone secretion. Therefore, sleep/wake cycles would be coordinated with the environment without temporal representation.

If we accept Burge's analysis, then the CIRCADIAN and AMAKIHI cases involve temporal representation. However, this forced interpretation has led to criticisms of Burge's proposal.⁸ These cases of temporal coordination are explainable without attributing temporal representations to these organisms, therefore, to paraphrase Peacocke (2017), the richer interpretation demanded by Burge's analysis violates a content-theoretic version of Morgan's Canon.

While appeals to Morgan's Canon are controversial (Fitzpatrick 2018), the appeal here relies on an understanding of representational explanation in cognitive science. According to Burge, and these critics of his, representational explanations in psychology provide explanatory and predictive power that non-representational explanations lack.⁹ The application of Morgan's Canon here is one of explanatory demand. If there is no behaviour whose explanation requires a representational explanation, yet the analysis of representation is such that it demands that we provide a representational explanation, then there must be a problem with that analysis of representation. It would undermine the role of representational explanations in cognitive science. Therefore, there is an inference to the best explanation at work here. Burge's analysis does not provide attributions of temporal representation with distinctive explanatory powers; therefore, it is Burge's *analysis* of temporal representation that is being rejected since it is too liberal. If his analysis is rejected, then the first-order explanation of temporal coordination in animals afforded by that analysis are also rejected.

If Burge's proposal is too permissive, then we should look for something more demanding. Peacocke (2019) argued that an animal capable of temporal representation must exhibit *representational preservation*. For an animal to exhibit representational preservation, it must have the capacities to (i) represent the current state of the world; (ii) represent a later state of the world as it acquires more information; and (iii) it must appreciate the temporal interval separating these states of the world. Temporal representation, for Peacocke, is a means of relating distinct representations of the world. According to Peacocke, an animal capable of representational preservation will be capable of behaviours that cannot be given a deflationary interpretation.¹⁰

Peacocke describes one such behaviour. Imagine a bird that feeds on prey that emerges from its nest at regular intervals. Suppose the bird has information about the prey's initial location, its direction of travel, and speed. In order to catch this prey, the bird must perform a calculation over these variables along with information about how much time has passed in order to know where the prey is. According to Peacocke, "the creature's mental states with durational contents [...] form an *essential component of the explanation* of the creature's representation of the likely current location of its prey, and hence of the creature's action." (Peacocke 2019: 220, emphasis added). According to Peacocke, temporal content is essential here, so appeals to Morgan's Canon do not favour the deflationary explanation since no deflationary position is available.

⁸ Gross (2017) and Peacocke (2017; 2019) directly respond to Burge with this criticism. Hoerl & McCormack 2018 do not directly address Burge but criticize similar accounts.

⁹ See discussion in Brown (2022) and Burge (2010).

¹⁰ Hoerl and McCormack (2018) make similar points.

Yet, despite Peacocke claiming the contrary, the same deflationary strategy used in the amakihi case applies here. The bird in Peacocke's example could know the prey's direction of travel and then associate a distance with some state of an internal time-dependent process. The bird may learn *if some time-dependent process is in state X, then travel Y distance*. No temporal representation is needed.¹¹

The point generalizes. Models of temporal cognition must include some means of keeping track of time through some time-dependent process. Deflationary theorists can simply provide non-representational interpretations of how these time-dependent processes are exploited through associative processes. This move is always available.¹² If attributions of temporal cognition are only warranted when confronted with behaviours that necessitate temporal representation for their explanation, then attributions of temporal cognition would never be warranted.¹³

In the next section we will articulate an alternative account of temporal representation such that existing empirical evidence can be utilized in an inference to the best explanation to distinguish between deflationary explanations and those involving temporal cognition.

3. Temporal Representation: Systematic, Flexible, and Transferable Use

A key point to notice in the debate so far is that explanations of temporal coordination that appeal to temporal cognition invariably appeal to time-dependent processes that constitute the mechanisms by which temporal coordination is brought about (e.g. oscillators, accumulators, etc.). We should not be looking for accounts of temporal cognition that do not employ time-dependent processes. Rather, what is needed is an analysis of temporal representation which distinguishes between the mere exploitation of time-dependent processes from the use of time-dependent processes to represent time.

This section aims to specify a cluster of behaviours that are prototypical for systems that employ time-dependent processes *as temporal representations*. The detection of this cluster of behaviours provides us with evidence for an inference to the best explanation that the animal in question is employing temporal cognition.

To illustrate these prototypical behaviours, consider the following two cases:

LEAKY FAUCET: Suppose a faucet in your house leaks. So, you place a bucket under the leak to collect the water. The leak is stable, so the bucket fills at a regular rate, about once per day. The weather is also very dry and hot, so your pot of basil needs watering every 24 hours. When the bucket is full, you pour the water into the basil pot. In this way, your action of pouring the water is coordinated with the time-sensitive needs of your plant through your learning a rule: *when the bucket is full, water the plant*.

¹¹ See Hoerl and McCormack (2018) for a deflationary strategy of this type.

¹² A similar point is made in Brown (2022).

¹³ Our discussion is restricted to cases of temporal coordination. Other capacities, like language, may require temporal cognition, yet for our purposes we are excluding those cases.

CLEPSYDRA (water clock): You place a bucket underneath a trickle of water. The water leaks at a regular rate, so the water level in the bucket carries information about the amount of time that has passed since the bucket was last emptied. You exploit this informational relationship as you use the bucket to keep track of and represent the passage of time. You know that your basil plant needs watering every 24 hours. Using the bucket to measure time, you water your basil plant. In this way, your action of pouring the water is coordinated with the time-sensitive needs of your plant through your learning a rule: *when 24 hours have passed, water the plant*.

In both cases the very same physical processes are occurring, water drips into a bucket at a regular rate, these processes are exploited for temporal coordination. There is no physical or mechanical difference between the systems. Yet, the clepsydra represents time whereas the leaky faucet is merely a system undergoing some time-dependent changes. Therefore, we cannot distinguish between a mere time-dependent process and a temporal representation on the basis of their dynamics (or their mechanical decomposition). Rather, the distinction has to do with how those processes are *exploited (or used)* for guiding behaviour.

However, not any exploitation of a time-dependent process suffices for temporal representation. As we saw with Burge's proposal, some characterizations of temporal representation are too permissive. The leaky faucet brings about temporal coordination by exploiting how processes unfold in time and *associating* specific actions with specific states of those processes. This is a temporal sensitivity without temporal representation.

As argued in the previous section, any token case of temporal coordination that can be explained through temporal cognition can also be given a deflationary explanation. We cannot distinguish between cognitive architectures involving temporal cognition and those that do not by appealing to individual behaviours. Instead, the difference between mere time-dependent processes and those that represent time centres on how those processes are exploited to guide further behaviour. In what follows, we describe a cluster of behaviours that are enabled by the *representational use* of a time-dependent process. Deflationary explanations could, in principle, account for these same clusters of behaviours, but in order to predict these behaviours they would have to make additional assumptions that do not follow from their simple associationist models. The representationalist account readily explains and predicts this cluster of behaviours. If this cluster of behaviours is found in an animal, then this gives us empirical evidence that they are capable of temporal representation.¹⁴

Consider the clepsydra again. This system has the very same dynamics as the leaky faucet, yet it is used *as a clock*. Several features of the clepsydra's use are distinctive.

First, the use of the bucket as a clock allows the bucket to represent temporal intervals that were not present in any associative context. We may calibrate the clock against a standard event so that the bucket fills after a specific duration. Yet our use of the bucket to represent time goes beyond this merely calibrating association. We can *systematically* use intermediate states of the bucket to measure intermediate temporal intervals (e.g., when the bucket is half full, it represents half the amount of time as the full bucket, etc.). Yet if the bucket is simply used to cue an associated behaviour, then there is no automatic interpretation or use that can be assigned to these intermediate stages. Call this feature *systematic usage*.

¹⁴ An alternative argumentative strategy that we could have adopted is to argue for a sufficiently developed theory of content, then apply that theory to cases. However, given that theories of content are incredibly controversial, any conclusion we could derive from such a strategy would be equally controversial.

Second, the use of the bucket as a clock allows for flexibility in what is measured. There is no restriction to measuring time for specific actions or tasks. Flexibility can appear as either a within task or across task property. Within task flexibility is the ability to measure time for coordinating various actions within a single task (e.g., with the same goal fixed). Across task flexibility is the ability to measure time for coordinating various actions across distinct tasks. In the Leaky Faucet case, the association is between the bucket's being full and watering the plant. There is no rational means for extending the use of this bucket to other activities. Yet, while the clepsydra may be calibrated by a specific event, it can be used to time various types of events for a single (within task flexibility) or various (across task flexibility) purposes. The representational use of the clock goes beyond those associative contexts in which the clock was calibrated. The use of the bucket as a clock allows us to time a variety of actions and events, yet the non-representational use of the bucket is restricted to specific actions (i.e., watering the plant). Call this feature *flexible usage*.

Third, information about time carried by the clepsydra can be exploited in further time relevant computations. Rates, or temporal densities, can be calculated from information about duration and number. Temporal orderings can be calculated from temporal interval information. Distances can be calculated from duration and velocity information. The temporal information that a clock carries can be used in rational processes to represent other features of the world. The associations involved in exploiting a time-sensitive process in non-representational ways do not give rise to these computations. Call this feature *informational transfer*.

A time-dependent process that is used as a clock contributes temporal information to the cognitive economy, thereby enabling systematic, flexible, and transferable use. This, we argue, is the mark of temporal representation. Importantly, our claim is not that any system capable of temporal cognition must exhibit systematic, flexible, and transferable behaviours. Rather, the claim is that if a system exhibits these behaviours, then that system possesses temporal representations that underpin those behaviours.¹⁵

Again, the point here is not that there is no deflationary reading of these behaviours. However, a system that exploits a mere temporal sensitivity does not automatically gain these functional capacities, since there is no guarantee that there will be some generalization beyond those associative contexts that establish the temporal sensitivities. Rather, these distinctive functional capacities can only be brought about by introducing further assumptions about the systematic, flexible, and transferable use of associative mechanisms. Without added evidence / explanation of these additional assumptions, then evidence of this behavioural cluster favours temporal cognition models.¹⁶

This epistemic criterion that we provide sets a 'high bar' for empirically establishing temporal cognition. Not any temporal coordination will suffice as evidence. Rather, the behaviours

¹⁵ Arguably we can use the bucket as a clock since we can mentally represent time. The clepsydra's temporal content might be derived from our capacity for temporal cognition. However, that's not available in the psychological case and that is not what we argue for. The notion of mental representation that we are developing here is in line with a variety of hybrid information-theoretic and consumer-based accounts of perception (e.g., Dretske 1981; Neander 2017; Shea 2018) according to which use is partly determinative of content.

¹⁶ Yet once those assumptions are made, the time-dependent process will have all of the hallmarks of a clock, and the difference between deflationary architectures and temporal cognition simply becomes a verbal difference.

described here are ones that distinguish between representational and non-representational uses of time-dependent processes.¹⁷

Our discussion so far has distinguished between mere temporal sensitivities and temporal representations but has said nothing about a representation's being *cognitive*. We want to avoid this thorny issue of distinguishing cognition from perception. However, we will note that a common feature of cognition is that of stimulus independence. Perceptual representations and perceptual processing are tied to sensory stimulation and the short-term memory systems employed by perceptual processes (Beck 2018; Phillips, 2019). While it's debated how long of a temporal interval these memory systems encode, most formulations provide a maximum of several seconds (see discussion in Clarke & Beck (2023)). However, cognitive processes are not tethered to sensory stimulation in this same way. The cases of temporal coordination we describe below operate over longer timescales than those afforded by any perceptual memory systems, and therefore involve cognitive processes.

4. Temporal Cognition in Wild Chimpanzees

In this section, we describe the hunting and foraging behaviours of the Taï chimpanzees, which live in the Taï rainforest in the Côte d'Ivoire (Boesch, 1994a, 1994b, 1994c, 2002, 2005, 2003; Boesch and Boesch-Achermann, 2000; Boesch, Uehara, and Ihobe, 2002). It will be shown that these behaviours exhibit the hallmarks of temporal cognition outlined in the section above.

The Taï chimpanzees are omnivores. While they forage for food, they also engage in hunting behaviours that predominantly target red colobus monkeys, which are medium-sized primates found in the upper strata of the Taï forest canopy. Colobus monkeys are far smaller and more agile than the larger chimpanzees, and therefore, individual chimpanzees have very low chances of catching this prey. Instead, these chimpanzees engage in group hunts (representing 77% of all hunts among Taï chimpanzee) that on average last a total of 16 minutes. Within the hunt, individual chimpanzees have distinct roles (Boesch 2002).

After locating the Colobus monkeys through auditory cues (Mine et al, 2022), an individual within the chimpanzee group assumes the role of the *driver*. The driver chases the prey and influences the prey's movement through the canopy. Other chimpanzees assume the role of *blockers* who present the prey from fleeing in certain directions, thereby allowing the driver to direct the prey along a specific path. The role of the blockers and driver is to control the prey's movement. Another chimpanzee, the *chaser*, directly pursues the prey and attempts a capture.

In the eventuality of the chaser's failure, a final chimpanzee, the *ambusher* secretly positions themselves further along the prey's trajectory to intercept and capture the prey. The ambusher does this by observing the position of the colobus monkey, along with the other members of the hunt, and then anticipates where the prey can be successfully intercepted by calculating the path the prey will take in response to the chaser and blockers. The ambusher then, losing visual contact with the others in the hunt, proceeds to an appropriate spot for an interception.

¹⁷ We do not look at cases of temporal cognition in order to determine what makes a cognitive system a temporal representation. Our worry is that this strategy requires a means of distinguishing organisms capable of temporal cognition from those that are not. This would require an account of the type being developed in this essay, and therefore, without such an account this strategy is not available. Thank you to a referee for raising this point.

This elaborate choreography of roles and actions necessitates an intricate interplay of cognitive faculties. However, our focus here will be on the capacities exhibited by the ambusher, and in particular their ability to anticipate the path of the prey in order to position themselves in a place for an ambush.

Here is Christophe Boesch (2001, pp. 100–101) describing the skills of a successful ambusher:

[the ambusher] not only has to anticipate the direction in which the prey will flee (recorded as a half anticipation), but also the speed of the prey so as to synchronise his movements to reach the correct height in the tree before the prey enters it (recorded as a full anticipation)[...] We also recorded a double anticipation when a hunter not only anticipates the actions of the prey, but also the effect the action of other chimpanzees will have on the future movements of the colobus, that is he does not anticipate what he sees (the escaping colobus), but how a future chimpanzee tactic will further influence the escaping monkeys.

Simply learning the trajectory of the prey is not enough to succeed in the hunt (what Boesch termed a case of ‘half anticipation’). Rather, success requires that the ambusher learn the trajectory of the prey and be able to predict where along that trajectory the prey can be intercepted given the ambusher and prey’s current locations and their relative speeds (what Boesch called ‘full anticipation’ and ‘double anticipation’).¹⁸

This ambusher behaviour exhibits systematic, flexible, and transferable use of temporal information. Since the arrangement of hunts can vary (e.g., number of participants in the hunt, location of the blockers, layout of the forest, etc.), the ambusher cannot have simply associated specific initial conditions with specific actions. Rather, the ambusher must exhibit some (within task) *flexibility* by adopting different action plans and initiating those plans at the appropriate moment in time based on the specific needs of the hunting scenario. One hunt might require that the ambusher move quickly in one direction, while another hunt might require the ambusher moves slowly in another direction. Similarly, given that the dynamics of the hunts vary given environmental factors, the ambusher cannot have simply associated the execution of an action plan with a specific state of an internal time-dependent process. Rather, it must be able to *systematically* choose when to act, in a manner that goes beyond associative contexts. Finally, in order to anticipate the trajectory of the prey, and where to intercept the prey, the ambusher must *transfer* information about the prey’s location, velocity, and time in order to calculate its own trajectory and acting timing.

These hunting behaviours exhibit the hallmarks of an animal employing temporal representations to coordinate their actions with the timing of events around them at the timescale of several minutes. Our next example looks at the foraging behaviours of the same Tai chimpanzee which exhibit these very same hallmarks, but over much longer timescales.

Besides hunting, the Tai chimpanzee also forage for fruit (Janmaat, 2019). The rainforests in which the Tai chimpanzees live are inhabited by a large number of foragers that compete for fruit (Houle et al., 2007; Zuberbühler and Janmaat, 2010). Competition is intense and given the size of the Tai chimpanzees and the number of chimpanzees that live together, they have the additional challenge of locating plants that regularly produce enough fruit to provide for the

¹⁸ Boesch (2002) notes that 32% of the 262 observed hunts involved either successful full or double anticipations. This performance is complicated not just by the need for temporal and spatial coordination, but also complex social cognition, and complex motor behaviours.

whole community (Janmaat et al., 2013a; Janmaat et al., 2013b; Ban et al., 2014; Janmaat et al., 2014; Ban et al., 2016).

It's been observed that the Tai chimpanzees can learn which fruit trees become ripe at specific times of the year. Some have argued that this memory for which trees fruit when shows that these animals are capable of temporal cognition (Janmaat 2010). However, deflationary explanations are readily available for these behaviours. The foraging animals may simply have associated the presence of ripe fruit at locations with the occurrence of other non-temporal features of the environment (e.g., they may associate a fruit's presence in a particular location with features of the environment, such as the changing colour of vegetation, intensity of rainfall, etc.). No appeal to temporal content seems needed in these cases. However, there is more to their foraging that we can point to which exhibits the behavioural hallmarks outlined above.

Of the available fruit in the forest, some are more highly sought than others. For instance, since figs are not only highly sought after but are only ripe for a limited time, there is a higher chance of figs being consumed by competing foragers than there is for other fruit (Shanahan et al., 2001). Drawing on previous work showing that Chacma Baboons leave their sleeping cliffs earlier during fig season to arrive at their foraging site before others (Noser and Byrne, 2007), Janmaat investigated whether Tai chimpanzees also alter their foraging behaviours depending on the type of food available (Janmaat 2019).

Unlike the Chacma Baboons, Tai Chimpanzees are almost entirely nomadic. One might have thought that knowledge of fruiting trees would influence the location of night nests, however, Janmaat found that it did not. Instead, knowledge of fruiting trees and journey-type influenced when they would leave their nest sites to arrive at their foraging locations.

When the Tai chimpanzees, particularly females with offspring, are foraging for less desirable low-competition fruit they avoid departing early when they would have to make a dangerous journey along the forest floor in the early morning hours. This delay could be up to two hours after sunrise. However, if the journey is short, and the chimpanzees can safely travel through the trees, they do not delay their departure, since they would not have to risk the early morning journey along the forest floor.

However, when the fruit in question are figs, the pattern of departure is strikingly different. In these cases, if the chimpanzees wait until the journey is safe, then the figs will have been eaten. What was observed was that regardless of how far away the fig trees were from the nesting site, the foraging chimpanzees would arrive at more or less the same time in the morning for breakfast. They would do this by adjusting their time of departure and their travel speed given the distance and the type of journey separating their nesting site from the figs – leaving earlier and travelling faster the further away the figs were (Janmaat 2019).

What then explains the chimpanzees' departure time when foraging figs? It is unlikely that local sensory cues could be guiding their behaviours. When fruit is ripe and nearby, cues like smell or appearance can serve to initiate foraging, and as a result this temporal coordination would be the result of a sensitivity to something other than time. Yet, in the wild, foraging sites can be as far as 900m away (Janmaat et al., 2014), therefore, immediate sensory cues cannot initiate departure. Neither could events such as sunrise, since departure times vary by several hours depending on the location of the fruit. Rather, something else allows the chimpanzees to keep track of their departure time in a way that is responsive to the time it takes them to travel to their feeding sites.

The chimpanzees seem to have an appreciation of which fruits are available, where those fruits are located, and the distance and type of journey that separates their nest location from the

fruit. This information is then used to determine when an appropriate time would be to leave the night nest in order to arrive at the feeding location at a relatively fixed time of the day before other foragers. It is this behaviour that provides evidence for temporal cognition.

The Tai chimpanzees have a means of keeping track of time that allows for a (within task) *flexible* form of temporal coordination. While the end goal of their actions, i.e., feeding, is the same, the means by which they bring about this action varies. They do this by implementing a range of action plans, navigating through the forest in various ways, to arrive at the appropriate location at the correct time. Their temporal coordination is also the product of a psychological process that requires *informational transfer* about time. They know when to arrive at the feeding site, they know how far the feeding site is, and they have some understanding of the sort of journey that they will take. All of this information is utilized to calculate *when* they will depart from the nesting sites and their travel speed. The chimpanzees are also able to systematically exploit this temporal information in that they are able to successfully adjust their departure time despite facing novel combinations of nest location, feeding location, and journey types. These features all go beyond any associations that may have been formed relating specific nesting sites with feeding locations.

The cases that we have pointed to involve complex cognitive achievements on the part of the ambushing and foraging chimpanzees. Focusing on the hunting cases, it is an open question what cognitive resources, in addition to temporal cognition, are needed for them to perform their specific roles and coordinate as a group. There is evidence suggesting a positive correlation between age of the ambusher and hunting success rates (Boesch 2002), which could be taken to indicate that hunting is an acquired skill. Yet, this does not tell us, by itself, whether temporal cognition is innate or acquired. Our aim in this paper is to establish that these animals have the capacity for temporal cognition. It is a further explanatory task to determine what grounds this cognitive capacity.

At this point, one might worry that other intercepting behaviours do not require temporal representation, and therefore, neither should these.¹⁹ Consider what it takes to catch a flying ball. The catcher sees the ball in the air and then moves their body to intercept the ball. A sophisticated explanation of this capacity appeals to a person seeing the ball's location and velocity, then calculating the ball's trajectory and deciding on an action plan. However, a much simpler process seems to be at work whereby people employ a simple heuristic to guide their movements. By keeping the ball at a fixed location in their visual field as they move (i.e., zeroing out optical acceleration), they will keep pace with the ball (Michaels & Oudejans, 1992). No temporal representation or trajectory estimation is needed. However, this strategy requires constant sensory contact with the target. Since that is not present in our cases, this deflationary strategy is unavailable.

So far, our evidence has been purely behavioural. However, in the previous section, we characterised temporal representations in terms of the use of temporal information carried by time-dependent processes. One might worry that we cannot infer that there are such mechanisms or processes from behaviour alone, since without independent evidence of the appropriate psychological mechanisms we would be unable to say how temporal coordination in these cases is brought about.

Our argument is predominantly an inference to the best explanation. In the last section we argued that if an organism's behaviours exhibit flexible, systematic, and transferable use of

¹⁹ Thanks to a referee for raising this point.

temporal information, then we have good reasons for thinking that their cognitive processes operate over representations of time. While mere deflationary explanations of temporal coordination could explain specific cases of temporal coordination, they cannot explain these behavioural capacities that go beyond associative contexts. However, if it were simply a mystery how such time-dependent processes could be physically implemented in biological systems, then we might suspect that something has gone wrong with our argument. Essentially, the temporal cognition explanation would no longer be the best explanation.

Luckily, the literature on the neurobiology of timekeeping has provided us with various possible mechanisms that may play this role in temporal coordination. The foraging behaviours that we described involved temporal coordination with specific times of day. Two distinct strategies for this coordination have been isolated in the literature. The first involves circadian oscillator mechanisms. It is well known that all mammals possess a central circadian clock located in the suprachiasmatic nucleus of the hypothalamus which carries information about the time of day for the guidance of behaviour (Bechtel 2011; Viera 2020). Another strategy involves interval timing strategies according to which animals time their behaviours by keeping track of the temporal intervals separating events. This would allow for time-of-day coordination by tracking interval lengths relative to a fixed time of day (e.g., sunrise). Possible interval timing mechanisms have been located in various parts of the brain, but lesions to the basal striatum impair timing at the scale of multiple minutes in laboratory settings. The basal striatum is thought to include oscillatory mechanism that allow for interval timing (Coull, Cheng & Meck 2011). These very same mechanisms could underpin the interval timing behaviours involved in the ambushing behaviour described above.²⁰

The foraging and hunting behaviours of the Tai chimpanzees show that they must be making use of the temporal information carried by time-dependent processes to coordinate their behaviours. In the previous section we argued that this is the hallmark of using a time-dependent process as a temporal representation. Since these are also cognitive mechanisms, we have reasons for attributing temporal cognition to these animals.

5. Generalizing Beyond Chimpanzees

Our aim in this paper is to establish that apes are capable of temporal cognition. Our case studies, however, have focused entirely on Tai chimpanzees. The aim of this section is to generalize beyond the Tai chimpanzees to apes in general.

In both the foraging and hunting examples the chimpanzees deploy temporal cognition in order to coordinate their behaviours with dynamic features of their environment that are beyond direct sensory range. Not only do the Tai Chimpanzees inhabit an environment in which ecological pressures allow their capacity to manifest, but they are a population which has been closely studied, thereby providing us with the relevant data.

Several other species of primates also inhabit similar environments and must coordinate their behaviours with dynamic and contingent features of their environment, so would seemingly be good candidates for possessing temporal cognition. For instance, Skywalker gibbons often

²⁰ It is likely the case that temporal cognition relies on multiple timekeeping mechanisms & systems. We have only described a selection here. If the same timekeeping mechanism is employed in the foraging and hunting behaviours we described, then this mechanism would exhibit across task flexibility.

forage for food far from where they sleep. While returning to their nests before sunset, they travel at faster speeds when they must cover longer distances, in order to return before sunset (Fei et al., 2022). They also depart earlier in the morning to arrive at high valued, ephemeral, but distant, fruit compared to lower value, stable, but closer, grass foraging sites (Fei et al., 2023). In both cases, researchers were not looking for the hallmarks of temporal cognition outlined above but given the evolutionary proximity of baboons to chimpanzees and the similar ecological challenges, we might expect them temporally coordinate their behaviours in similar ways by employing temporal cognition. We simply need to look.

Aside from feeding, social dynamics also require temporal coordination. The Sumatran orangutan, for instance, lead largely solitary lives in dense tropical forests. Dominant flanged males are known to produce long-call vocalizations which can be heard up to 1.5km away and indicate the future travel direction of the male. When the calls are made at night, these calls also indicate the travel direction of the male the following morning (van Schaik et al., 2013; Spillman et al., 2015; Askew et al., 2016; Lameira & Call, 2018). When these long calls are heard by subordinate males, these males avoid the indicated direction of travel of the dominant male. Receptive females, on the other hand, will follow the direction of travel indicated by the long call to stay within close proximity of the dominant male, either to avoid harassment by subordinate males or to mate. Some data suggests that female orangutans stay within close proximity of the dominant males by intercepting the male's trajectories over the course of several hours (e.g., see the case of Ani and Arno in van Schaik et al., 2013). However, a closer analysis of the original data would be needed to make the statistical point.

Multiple cases of these kinds can be found in the primate cognition literature. We find animals capable of complex spatial cognition and some form of temporal coordination with dynamic and contingent features of the environment. Yet we lack the fine-grained data to conclude that this temporal coordination is brought about by temporal cognition as is the case with the Tai chimpanzees. Yet, given the similar ecological challenges and evolutionary similarities, we have some reasons for thinking that it is likely that other apes beyond the Tai chimpanzees are also capable of temporal cognition.

6. Conclusion

We have argued that apes are capable of temporal cognition. As was argued in sections 2 and 3, in order to show that some creature is capable of temporal cognition we should not be searching for evidence of some behaviour that cannot be given a deflationary explanation. The deflationary strategy for any individual behaviour is always available. Instead, the argumentative strategy involves an inference to the best explanation. The best explanation of behaviours that exhibit flexible, systematic, and transferable use of temporal information is that those behaviours are underpinned by representations of time. In section 4, we argued that the Tai chimpanzees exhibit hunting and foraging behaviours with these features.

Section 5 argues that it is likely that other apes are also capable of temporal cognition given their capacities for temporal coordination. The section also specifies what evidence would be needed to confirm that claim. While it is not guaranteed that other apes perform these activities by employing the same cognitive capacities, the evolutionary and environmental similarities make it likely that they too employ temporal cognition to coordinate their activities in time.

The argument developed in this essay also allows us to see how capacities for temporal cognition can be empirically studied across the animal world. By setting a 'high bar' for evidential support, we avoid the problem of overly anthropomorphizing non-human animals by

too liberally attributing to them sophisticated cognitive capacities. Yet we also avoid the pitfall of requiring some critical test in support of the theory.

This was a positive argument that these animals are capable of temporal cognition. What then do we say to those authors that have argued that temporal cognition is a uniquely human capacity? Two options are available. One option is that the claims those authors made, according to which temporal cognition requires a uniquely human cognitive capacity, such as language, complex causal reasoning, or episodic memory, are simply false. Temporal cognition can exist independently of those other capacities. Another option is that we accept the claims of those authors, yet we see this evidence for temporal cognition in non-human animals as evidence that these animals are also in possession of these other cognitive capacities.

How we choose to respond to this question is one that requires further work. Our argument has aimed to simply show that apes are capable of temporal cognition. We have not said anything about whether other psychological capacities, for instance causal reasoning, might be needed to underpin temporal cognition. We also have said nothing definitive about the development of capacities for temporal cognition. However, we have articulated methods for determining which animals are capable of temporal cognition, which is a first step towards answering these other questions.

Yet, we think that a general lesson can be taken from the argument in this paper. When it comes to determining whether some animal, human or non-human, has some cognitive capacity, we should not look for some behaviour or experimental evidence that unequivocally settles the issue. Deflationary and alternative explanations are always available.²¹ Rather, we should let our theorising guide how we develop our empirical investigations so that we can formulate an inference to the best explanation, rather than an inference to the only explanation.

Acknowledgements

We are grateful to the editors of the Australasian Journal of Philosophy for their assistance, and to two anonymous referees for their constructive comments. We also want to thank Albert Newen, Alfredo Vernazzani, and Carel van Schaik for their feedback on previous versions of the paper.

We also obtained very helpful feedback from presenting aspects of this material at the following venues: the Inaugural Meeting of the Philosophy of Animal Minds and Behavior Association (UNED Madrid, April 26-28, 2023), the Mind and Cognition Centre research meeting (Ruhr-Universität Bochum, June 29, 2023), the Philosophy, Psychology and Informatics Group (PPIG) (University of Edinburgh, November 15, 2023), the CIFAR Neuroscience of Consciousness Winter School (Cancùn, Mexico, December 13-16, 2023) and the University of Sheffield (May 15, 2024).

²¹ This is not merely a point about the logic of underdetermination. This is a special point about cognitive science. The mind is an incredibly complex black box. There are always plausible alternative theories.

Funding Information

Angelica Kaufmann's research was supported by the DFG-project (NE 576/14-1) "The structure and development of understanding actions and reasons" (Gefördert durch die Deutsche Forschungsgemeinschaft [DFG] – Projekt NE 576/14-1).

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