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Non-human primate token use shows possibilities but also limitations for establishing a form of currency

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Non-human primates evaluate choices based on quantitative information and subjective valuation of options. Non-human primates can learn to value tokens as placeholders for primary rewards (such as food). With those tokens established as a potential form of 'currency', it is then possible to examine how they respond to opportunities to earn and use tokens in ways such as accumulating tokens or exchanging tokens with each other or with human experimenters to gain primary rewards. Sometimes, individuals make efficient and beneficial choices to obtain tokens and then exchange them at the right moments to gain optimal reward. Sometimes, they even accumulate such rewards through extended delay of gratification, or through other exchange-based interactions. Thus, non-human primates are capable of associating value to arbitrary tokens that may function as currency-like stimuli, but there also are strong limitations on how non-human primates can integrate such tokens into choice situations or use such tokens to fully 'symbolize' economic decision-making. These limitations are important to acknowledge when considering the evolutionary emergence of currency use in our species.

This article is part of the theme issue 'Existence and prevalence of economic behaviours among non-human primates'.

1. Introducing tokens to primates

We have five goals in this paper. First, to provide a brief overview of projects that introduced tokens as relevant stimuli in tests with non-human primates. Second, to describe what we see as qualities of token systems that are necessary to argue that tokens may function as a form of currency for non-human primates. Third, to define the cognitive pre-requisites we see as necessary for understanding those qualities of tokens and using tokens in ways aligned with those qualities. Fourth, to summarize what the successes and limitations of empirical studies using tokens with primates mean for the possibility that a currency system could be understood and used by non-human primates in ways consistent with modern humans' economic systems. Fifth, to discuss whether the limitations we see are fundamentally the result of cognitive limitations or are the result of environmental constraints that have limited the utility of currency in such a way that no other species besides humans have needed to incorporate such a system into social interactions.

To those interested in comparative cognition, these goals will be easy to appreciate as providing insight regarding animal behaviour and the cognitive abilities that may or may not exist in other species to support that behaviour. To others who may not see the relevance of studying economic behaviour in non-human animals, we suggest that examining the cognitive pre-requisites for a currency system is made possible via an evolutionary lens and specifically through research with our closest-living relatives, the primates. Human behaviour and cognition, like human bodies, have evolved through adaptation to selective pressures introduced by environmental change. In the case of human economic behaviour, including the ability to understand and develop systems of currency, there are core cognitive competencies at work that almost certainly existed prior to the emergence of modern-day economic behaviour. Thus, it is an important question for understanding the emergence of human economic behaviour to understand what cognitive precursors may be necessary to engage in such economic behaviour. Comparative research is ideal in this pursuit for two reasons. First, humans are unique in the degree to which they can use systems of currency to aid economic behaviour, but they are not unique in terms of their general cognition. Thus, what has allowed humans to develop currency systems may involve specific cognitive capacities that animals struggle to demonstrate. A comparative framework can highlight those specific capacities (phylogenetically) as a complement to what developmental studies might also highlight (ontogenetically). Second, a comparative perspective allows one to see the potential component behaviours that may have existed in other species (including humans' ancestors) before they combined to produce new capacities in a species that faced a unique selective pressure to adapt those behaviours (in this case, adoption of systems of currency). Adult humans routinely engage in the behaviours and cognitive processes we outline in this paper. This is non-controversial. They understand that coin size and coin value are not related (in many currency systems). They accommodate value of items and quantity of items (e.g. preferring two $10 bills over 16 quarters). They delay gratification to accumulate greater value. They can barter and exchange using arbitrary stimuli that are agreed-upon mediums to allow complex distributions of goods among diverse producers or purveyors of goods. This last point is reflected in the widespread use of token systems as forms of currency.

We focus here on arbitrary physical stimuli as tokens as they might inform a comparative perspective on this aspect of non-human primate economic behaviour. We think token use is particularly important in understanding the emergence of economic systems because tokens are manipulable stimuli like many of the earliest known forms of human currency [1,2]. They are collectible, transportable and capable of being used without need of any sophisticated form of linguistic exchange. They can be quantified and compared easily by species that rely heavily on vision. They are basically arbitrary in their material origin, but when used with animals are typically visually appealing and salient in their inherent physical properties, much like early currency systems (e.g. shells, rocks, gems, beads). We note that the structure of this article is not to provide a list of the sufficient capacities needed to confirm that a currency system exists for another species. Rather, we are proposing that there are some necessary cognitive pre-requisites that one needs to see evidence for in order to sustain a claim of *possible understanding of currency* in another species. We acknowledge that there are frameworks for currency systems that take as central to those systems aspects of social behaviour including norms and institutional practices, and other frameworks that focus on currency systems that operate as tools for individuals within those systems (e.g. [3]). We also acknowledge that there are important cognitive capacities that may be required for engaging in systems of currency with other individuals, including theory of mind and metacognition. We agree that these are important perspectives to also consider when taking a comparative perspective on the understanding and use of currency. Other sources, including other papers in this special issue, have addressed questions about other aspects of economic behaviour such as biological market theory (e.g. [4–7]), exchange of commodities between individuals (e.g. [8]), endowment effects (e.g. [9–11]), responses to inequity in exchange behaviour (e.g. [12]), bounded rationality (e.g. [13,14]), cooperative behaviour (e.g. [15–18]), bartering and exchange of tokens among conspecifics (e.g. [19–22]) and a host of other fascinating ideas and data from non-human primates (see [23]). These also inform our understanding of primate economies, but our expertise is in associative learning and assessment of cognitive faculties in non-human primates, areas for which physical token use can be extrapolated to thinking about economic behaviour and the question of whether other species can understand the idea of physical currency systems in a way that tells us about the evolution of monetary systems in humans.

We begin by outlining some of the history of using 'token economies' in non-human primates and some of the more recent attempts to integrate physical tokens in tests of primate cognition and behaviour. One of the earliest attempts to use a secondary reinforcer involved training chimpanzees to use tokens [24]. The chimpanzees learned which tokens could be used in a machine to obtain food, and they also learned to discriminate tokens on the basis of how much food they could get for each. Wolfe [24] noted the necessary temporal delays that tokens instilled between when chimpanzees obtained tokens and could use them to get primary rewards. He also suggested that tokens would make an excellent approach to look at delayed exchange behaviour. Tokens were then rarely used again in studies with primates until the end of the twentieth century, after which their use became widespread, as investigators came to realize their utility in asking a number of questions. Tokens were introduced as a way for primates to obtain food from investigators through exchange behaviour (e.g. [12,25–27]). They were used to determine if primates would work for those items so that they could be exchanged for food later at performance levels comparable to when food was given directly [28]. They were used to examine future-oriented behaviour, where tokens could be gathered before they could be used, to see if anticipation led to such collecting behaviour (e.g. [29,30]). They were used to see if primates would exchange tokens with each other, and perhaps selectively obtain tokens that were only useful to a partner (e.g. [19,31–34]), as well as to ask other questions about how token tasks might influence social behaviour of conspecifics (e.g. [35]). In many of these cases, one of the goals of the research was to determine whether tokens might share some features with currency systems (e.g. [26]). We now offer a perspective on how tokens would need to be used to suggest comparability to currency, and whether the evidence for such use is strong enough to draw that conclusion.

2. What makes a token a potential form of currency?

Currency is defined as anything that has the capacity to act as a medium for exchange, as a store of value and as a unit of accounting (e.g. [3,36,37]). In that reference frame, there are four qualities that a token system must have (and that users of tokens must be able to understand and calculate) to make tokens more equivalent to the various forms of historically and currently recognized currency (coins, beads, shells, bitcoins, satoshi and so forth). The first pertains to the idea of currency as a unit of accounting, and the quality is a commonly shared and agreed-upon scale for absolute and relative values of tokens. In other words, one has to know that two tokens are worth more than one token of the same type (the quantity representation) and that different types of tokens can have ordinally ranked quantitative values (e.g. black tokens can be exchanged for twice as much reward as white tokens just as dimes in the US currency system can be exchanged for twice as much as nickels) and ordinally ranked qualitative values (e.g. black tokens can be exchanged for better rewards than white tokens just as a dime allows you to purchase a better item than a nickel). In systems with two or more token types, there is also the need to represent value across token type and as a function of quantity of tokens of that type, so as to generate relative values (e.g. two black tokens are worth more than three white tokens just as two dimes are worth more than three nickels).

The second quality of a token system that could approximate currency is that there has to be recognition that these absolute, relative and combinatorial representations of value are, for at least the short term, stable. This means that across time, learned relations among tokens, the values of those tokens for exchange and the process for using those tokens must be remembered. This allows for the store of value noted earlier.

A third quality of token systems that could allow them to function analogously to currency systems is that users should appreciate not only that greater quantities of tokens have greater value but also recognize that tokens can be accumulated to increase their value for future exchange. Tokens must be treated in some cases as valuable through their collection and retention rather than their immediate exchange. Otherwise, immediate exchange or use of tokens as soon as they are acquired reflects a more likely associatively conditioned response that is heavily dependent on the secondary reinforcer properties of those tokens. To act in a meaningful (and valuable) way as a medium for exchange, there must be some temporal delay before obtained currency can be exchanged again, and during that interval, the currency must be viewed as having value. So, tokens would need to be used in a way that reflects this temporal component.

A fourth quality of token systems that could function as currency systems is generalization of use to new contexts, with highly varied primary rewards, and through use with familiar and novel exchange partners. In other words, the token system must be used flexibly and universally, and needs to be used by all economic agents in that system, regardless of their familiarity with each other. Money, for humans, can be used with anyone, for almost any desired reward that one wants to obtain, and users of money understand this. Equivalent token systems would require the same universality of use, thereby demonstrating their utility as a medium for exchange.

3. Cognitive pre-requisites for the concept of currency

Having defined what qualities tokens would need to have to be analogous to currency, we now discuss what we see as the minimum necessary cognitive mechanisms (and learning mechanisms) for non-human primates to understand the concept of currency. Some of these pre-requisites should be considered non-controversial and easy to accept as present in many primate species. First, we assume that learning mechanisms of the sort that associate arbitrary stimuli (sometimes called secondary reinforcers) with highly salient, important stimuli (sometimes called primary reinforcers) are required. We know that all tested primate species (as well as many other nonhuman species) show forms of associative learning, and we outlined above some successful attempts to introduce tokens as secondary reinforcers (e.g. [24]; also see [38]). Second, we assume that learning mechanisms and experiences of token exchange for reward must be encoded and stored in memory systems. Note that these memories do not need to be episodic (i.e. the agent does not need to remember that he or she previously had the experience of exchanging stimuli in a past consciously remembered event). Those memories can be encoded, stored and retrieved as more semantic knowledge or associative learning (i.e. that a token of a specific colour has led to preferred food) even after long delays (e.g. [39]). This means that one need not show episodic memory in primates (a controversial topic; see [40–43]) to argue that information about potential currency or partner quality is remembered. Third, we assume that primates can understand that tokens can be used to collect delayed rewards, and that collecting them in the present allows for delivery of some primary reward in the near future or perhaps even in the far future (e.g. [24,28,44]). Beyond these three pre-requisite learning and cognitive mechanisms, which we think are clearly in evidence in non-human primate species, all remaining pre-requisites are open to debate on the basis of empirical evidence, although we argue that in all cases, the evidence is at least suggestive of the ability to understand currency in a way that could reflect on the capacity to engage in true economic behaviour by some non-human primates. Here, we are focusing on aspects of physical cognition necessary to the emergence of a currency system, but we also realize that various aspects of social cognition (e.g. theory of mind) may contribute to the full-fledged economic systems that we observe in humans.

What would need to be demonstrated, and that cannot be taken for granted, is that non-human primates could interact and use tokens in a way that indicated that:

1. They appreciated that more tokens of a given type were preferred to fewer tokens. The cognitive process involved here is quantitative cognition for relative value.
2. They appreciated that different types of tokens could be associated with different quantities of a specific reward. The cognitive process involved here is quantitative cognition for absolute value.
3. They appreciated that differing token values or quantities of tokens reflected different expectations for effort, or time delay, to obtain those tokens. The cognitive process involved here is temporal discounting with the capacity for delay of gratification.
4. They appreciated that tokens represent the degree of reward cost or reward benefit in the context of making other choices, classifications, or judgements of unrelated stimuli. The cognitive process involved here is calculation of risk, reward and outcome probability for non-primary rewards.
5. They appreciated that token value and token quantity must be combined arithmetically to produce overall value estimates for a token array. The cognitive process involved here is quantitative computation, where multiple stimulus

dimensions including the absolute value of each token type are combined without attentional bias to one dimension over the others.

We next present some of the empirical data relevant to each of these necessary cognitive pre-requisites. Note that we are not arguing that evidence of these cognitive faculties is sufficient to claim that non-human primates understand the concept of currency systems. Rather, we argue that they are necessary to justify the possibility that such understanding of currency is possible. Later sections will include discussion of other factors that would need to be demonstrated to strengthen a claim that non-human primates understand the idea of currency as seen among humans.

4. Are non-human primates sensitive to token quantities as interchangeable for corresponding food rewards?

Given that non-human primates learn to associate arbitrary tokens with food items, the first question of relevance to our list of necessary qualities of token use as potential currency involves recognizing quantities of tokens as having relative and absolute values. The relative values would be demonstrated in showing that non-human primates spontaneously choose larger numbers of identical tokens over smaller numbers of the same type of tokens. Recognition of absolute value of tokens would require that non-human primates can compare tokens to the real rewards that they have been paired with in the token economy in such a way that the tokens generate cardinal (absolute) representations rather than ordinal (relative) representations. A number of studies have tested the ability of primates to associate tokens with food items so that quantitative comparisons and judgements could be made. Capuchin monkeys have participated in many of these studies. In one of the most thorough assessments [45], monkeys learned that different types of tokens represented one reward item or three reward items. Then, the monkeys were shown two options that included a single token worth three food items and from one to five of the tokens worth a single food item each. Four of 10 monkeys maximized the amount of food they could get across these trial types. However, four other monkeys preferred the token worth three food items, even when this was less food than could have been obtained from taking four or five of the single-item tokens. The last two monkeys showed the opposite bias, preferring the set of more tokens over the single token, even when this led to less food overall (e.g. selection of two single-item tokens versus one three-item token). Even more complicated comparisons (such as a choice between two tokens each worth three food items versus five tokens each worth one food item) led to biases and suboptimal responding, suggesting a real difficulty for the monkeys. Evans *et al*. [46] used a similar approach in which capuchin monkeys and chimpanzees showed only limited success in a token summation task. All primates first learned to choose correctly between containers holding one to five food items. Both species also selected higher-valued tokens presented against visible food items, indicating that tokens were viewed in terms of their absolute values. In the critical test trials presenting one three-item token against multiple one-item tokens, only two of four chimpanzees showed some flexibility in choosing the larger set of one-item tokens (summing their value) and no capuchin monkeys were successful in these trials. Thus, although primates are capable of representing and potentially combining the value of tokens within a discrete choice setting, this is a difficult task that reveals a limit to the abilities of primates to approach a token economy in the same manner as humans do on a regular basis, one in which tokens can be combined arithmetically to produce overall absolute value representations for a token array. This result reflects the limited ability of non-human animals to accurately represent cardinal (absolute) values when representing sets of larger numbers of things, compared to their fairly good abilities in representing ordinal (relative) values (see [47–50]).

Addessi *et al*. [51] conducted another insightful assessment of token quantification in capuchin monkeys. They presented the monkeys with all possible pairs of one to five food items or one to five tokens (each exchangeable for a food item). In both cases, the same relative performance pattern was seen, where more numerically similar comparisons (e.g. four versus five) were harder than less similar comparisons (e.g. two versus five), but overall performance suffered with tokens. This is problematic for claims that tokens can operate as currency because there is not equivalence in the discriminatory precision for token stimuli that must be present for such stimuli to operate as forms of currency as per our discussion above. Addessi *et al*. [51] reported that there were two possible explanations for the difference: tokens may have introduced a higher cognitive load than did food items, or the monkeys may have had decreased motivation to choose the larger number of tokens owing to the delayed feedback associated with token exchange. We agree that these are both viable explanations, but they also challenge the idea that tokens operate as a form of currency, at least in the way that currency is used by adult humans.

Some studies with chimpanzees have shown improved performance on this type of quantitative judgement of tokens. Beran *et al*. [52] trained chimpanzees that any given token was exchangeable for a single food item, and tokens varied in size, shape and colour. Chimpanzees then were presented with a choice of two token sets. Initially, the tokens were all presented simultaneously, but in subsequent experiments, they were presented sequentially into opaque containers, and so the chimpanzees had to sum the totals in each container without ever getting to see the total number of tokens in each set. Across all manipulations, chimpanzees chose the larger sets, largely ignoring the irrelevant physical dimensions of the tokens (i.e. they chose three small tokens over two larger tokens). However, a more telling limitation came from trials in which tokens were presented in comparison to sets of real food items. Importantly, in this test, the temporal delays to reward were held constant, so the potential motivational factor noted by Addessi *et al*. [51] was controlled. But chimpanzees performed less proficiently in choosing more tokens over fewer food items to choosing more food over fewer tokens. Although Beran *et al*. [52] argued that tokens were functionally interchangeable with food items overall, these selective differences are highly relevant to the question of whether tokens can truly operate as a form of currency. Perhaps part of this inability of animals to choose tokens over primary rewards reflects that those primary rewards serve as the unconditioned stimuli to which responses are naturally elicited, whereas tokens are necessarily conditioned stimuli, for which experience is required to elicit comparable responses to those made to unconditioned stimuli. From this perspective, it seems clear why tokens are more difficult to accurately judge in choice settings where quantity judgements are being made. Greater success in showing that quantitative information (how many) and qualitative value (what reward type) can be combined to generate clear behavioural choices that reflect the value of choice options likely requires removing the prepotency of primary rewards themselves from the choice set (see [53] for one compelling example of this).

An earlier study produced an even more consequential limitation in the quantitative processing of tokens. In that study [54], a rhesus monkey and two chimpanzees learned to associate arbitrary objects (different coloured plastic eggs) with different quantities of food (i.e. each unique colour of egg contained a consistent and different number of food items within it). These primates flexibly compared tokens of different value to one another, choosing the more valuable token. They also performed well in choosing between a set of tokens and a set of food items. They would, for example, choose two eggs that each contained four items in them over a set of six visible food items, but they would choose the six visible items over a single egg that contained four items within it. This result presses towards a conclusion that non-human primates may be able to flexibly calculate the overall value of currency-like stimuli on the basis of the magnitude ('how many eggs') and relative value ('how much in each egg of that colour') of the set. However, the chimpanzees could not differentiate between sets of eggs that differed in their quantity and value. For example, the highest value colour was selected even when compared with three or four eggs of a lower individual value. In this case, the default response was to choose based solely on the colour dimension, with an apparent inability to use information about the quantity of eggs in that colour as a means to accurately represent the sum total of food available. This result, again, presses towards the idea that cognitive load is too high in this case, even though comparing eggs to food sets was possible, or perhaps also an issue of prepotency to respond to highly valued stimuli. This result does contrast, however, with the success of a minority of capuchins (4 out of 10 monkeys) in Addessi *et al*. [45], although in that experiment, these were difficult trials even for those monkeys who showed some success. But this result does align with a conceptual replication attempt by Evans *et al*. [46] that showed once more that chimpanzees and capuchin monkeys could not accurately judge the objective value of token sets when token quantity and individual value of token type both needed to be included in the calculation. This result may have an analogue in the behaviour of humans, at least when they are young. Bruner and Goodman [55] reported that 10-year-olds showed an interesting bias when asked to estimate the size of either cardboard discs or coins of various denominations. Estimates for the discs were quite accurate, but children overestimated the coin size in proportion to the coin value (also see [56]). Thus, adult humans are better able to reconcile competing stimulus qualities than are children and non-human primates (e.g. value of coin (dime is greater value than a nickel) and size of coin (dime is physically smaller than a nickel)), which may be a byproduct of greater experience with monetary systems gained over a lifetime of learning coupled with greater cognitive capacities such as inhibitory skills and working memory. This would suggest that non-human primates may not be capable of engaging currency systems that involve two or more forms of tokens that need to be represented as to their individual values and their quantity (but see [53]). However, this does not mean that simpler systems with only one form of currency are beyond the capacity of other species.

5. Earning and accumulating tokens: evidence from tests of self-control

Tokens have also been introduced to studies of self-control, primarily with the goal of facilitating performance in the absence of prepotent, edible stimuli that can lead to impulsive behaviour rather than inhibited responding. For example, in the reverse-reward paradigm, subjects are required to select a food set that they do not want (lesser in qualitative or quantitative value) in order to receive a more valuable and thus more desirable food set. Chimpanzees eventually succeeded in this task when symbolic tokens (laminated cards with Arabic numerals) were used to represent the food sets versus edible rewards, which were arguably too prepotent for animals to engage with in these task-specific ways [57,58]. Tokens also facilitated performance by capuchin monkeys in the reverse-reward task, such that capuchin monkeys selected a token representing a smaller amount of food in order to receive a token representing a larger amount of food despite failures to inhibit responses towards the larger food sets [59]. Interestingly, tokens that represented a one-to-one correspondence (one token for every food item) versus a one-to-many correspondence (one token for a set of food items) did not facilitate performance for capuchin monkeys [59] or chimpanzees [60]. In these cases, primates maintained a 'choose larger' response, and thus the tokens failed to distract from the tempting nature of larger quantities despite being inedible. This is a limitation that links back to the quantity judgements reviewed in the last section.

In the classic intertemporal choice task, self-control is assessed by providing subjects with two food sets, one of which is lesser in value but can be obtained immediately and the other of which is more valuable but requires a delay to reward. Capuchin monkeys learned to associate food types with tokens, and when given a choice between low- and high-valued tokens, they selected the higher-valued token [61]. Some monkeys even selected higher-valued tokens over lower-valued, immediately available food rewards. This result matched a report of the same kind of test given to chimpanzees [62] in which those chimpanzees demonstrated self-control in the face of symbolically represented and delayed rewards. In this test, chimpanzees preferred the more valuable option when comparing two food rewards or two tokens representing food rewards and also obtained the objectively most preferred item when presented with choices of tokens and real foods even when the token exchange was delayed by several minutes. Thus, symbolic and analogue tokens may help to bridge performance in self-control scenarios in which inhibitory responses towards prepotent, edible stimuli are challenging. However, that is not always true, depending on the type of task along with the token type.

Tokens also have been integrated into delay of gratification tests that were adapted from developmental assessments of self-control with human children (e.g. [63]). One of these, the accumulation paradigm (also referred to as the delay maintenance task) introduces a preferred food reward to a subject, and that food amount continues to grow as long as the subject does not consume any of the items. This test has been used to assess self-control among a variety of primate species, with varying degrees of success in terms of the amount of time that an animal (or species) will wait for the growing food pile, with longer accumulation periods resulting in larger reward earnings (e.g. [64–70]). In some variations of this task, researchers have introduced tokens such that animals accumulate inedible tokens that they later exchange for an equal quantity of food rewards. Tokens are arguably less salient in that they lack the prepotent qualities that an animal may face in the presence of edible food rewards (as in the reverse-reward task), potentially increasing performance on the accumulation task when tokens are integrated. Contrary to this prediction, however, capuchin monkeys accumulated a greater number of food rewards than tokens and chimpanzees accumulated an equivalent number of tokens as they did food rewards [44]. Relatedly, when presented with symbolic tokens representing different quantities of food, capuchin monkeys and preschool-aged children exhibited a lower preference for the larger, later token when compared with choices made in the presence of actual food rewards [71]. It has been suggested that tokens facilitate self-control performance if they abstract away from the prepotent qualities of the rewards that they represent (e.g. [57,72]; see [71] for a discussion). This may be true for inhibitory control tasks such as the reverse-reward task. However, in the case of the accumulation paradigm, tokens that represent a one-to-one correspondence with edible food rewards do not improve performance as the 'choose more' rule governs choice behaviour even for inedible stimuli in these cases. These results suggest another limitation for connecting token use in primates to the possibility of a currency system being something they could truly understand.

6. Potential cognitive limitations involving tokens and unassessed abilities

Despite the positive evidence offered above for tokens being used to represent quantity and quality, and the evidence that in some cases tokens were treated as valuable items for later exchange that were worth waiting for (and allowing to accumulate), we believe that there are some clear limitations in how non-human primates may be able to process and represent more complicated (and longer-term) situations that would be essential to engaging in the use of a currency system that involved two or more value holders (i.e. two or more types of tokens, coins, etc. that each have a different value). With regard to tokens themselves, they are sometimes not treated as equivalent to primary rewards, and in some cases, this appears to affect choice behaviour and valuation of choice options. The quantity judgements studies we described all showed that discrimination acuity was poorer for tokens than for real food items. This may be a motivational difference rather than a cognitive limitation in some tests, but it cannot be for all of those tests. It also is possible (and, we believe, more likely) that tokens produce a cognitive load that is too strong for non-human primates to maintain the representation of value that reflects a true equivalence of currency to goods (primary rewards). If cognitive load does underlie increased difficulty in quantifying tokens and estimating their value relative to real rewards, this could highlight why humans are able to think about currency systems in unique ways, because humans have the 'extra' cognitive resources needed to deal with the load introduced by the use of non-primary currency stimuli. This is an empirical question, given that only a few studies of primate cognitive abilities have included measures of the effects of cognitive load (e.g. [73–75]). Future research that directly assesses how well tokens can be used under conditions of low and high cognitive load would be highly informative.

We note briefly that there may be other important cognitive capacities and social skills that are critical to engaging in systems of currency. These include higher-order cognitive and metacognitive abilities including theory of mind, if one considers that currency use requires knowing that other agents can engage in thinking that is different from the self. Human systems of currency also generalize across varied settings in which currency can be used. Adult humans understand that different currencies can be converted to each other and that currencies that are typically used in only certain settings can also be used in new settings. There has been little empirical work showing such broad generalization of token use in non-human species (but see our comments below on some studies in natural settings that may approach this generalization).

7. Are tokens a form of currency?

Money is funny. It is not a primary reinforcer, but rather is a unique secondary reinforcer [76], or perhaps something in between [3]. For most laypeople, currency means money, and so the question is whether any token system used with non-human primates meets the qualifications to be considered currency-like. We believe that the evidence does not support this conclusion. The reader may have noted that the preceding sections vacillated between stating that in some tests, token use seemed to approximate what one would expect if tokens were like currency but in other tests, performance revealed concerning limitations. Ultimately, these limitations are essential to acknowledge, as we noted at the beginning of this paper, that it is the limits in non-human animal behaviour that help define the nature of currency systems and how humans can engage those systems. Non-human primates may have cognitive limitations that will prevent them from integrating all of the necessary qualities of a currency system into their behavioural responses to tokens, and thus they cannot fully use tokens in the way that humans use currency. We also conclude that more assessments are needed to clarify the present uncertainty around these issues. Are primates incapable of understanding and using currency systems, or has there simply been no fair and proper encouragement to do that? It was long considered to be true that only humans could use symbols and engage in symbolic communication, but then ape language projects suggested otherwise [77–79]. Other 'higher order' cognitive abilities also were once considered to be uniquely human, but assessments of non-human primate theory of mind [80], tool use [81], prospective cognition [82] and metacognition [83–85] now indicate otherwise, or at least call into question the claim of humans' unique capacity for these things. With the proper structure, including immersion in environments in which tokens are essential to numerous daily activities as is the case for humans, we might see more facile use of tokens, and better calculation and judgement of their objective value and their possibilities as tools to engage in barter, cooperation and perhaps even the development of simple economies. These environments ideally would include multiple options for spending/exchanging currency, including options that were temporally delayed, and of varying cost in terms of currency required. They would include opportunities to gain currency at limited times, and to store that currency for later use. Ideally, these environments would include exchange opportunities with conspecifics involving primary and secondary rewards to embed the currency system within the social domain, where partners and perhaps rivals would also be using the currency system. Such an experiment would be very difficult to instantiate with captive primates. However, there may be natural settings in which some of these environmental features exist. Brotcorne *et al*. [86] reported a number of intriguing exchange behaviours among wild macaques that would steal from tourists and then barter for the return of taken items. In this setting, there are variable stimuli that serve as more or less valuable items to be bartered after acquisition. Bartering occurs after short delays, and individuals may be learning aspects of this 'economy' through observation [87]. More research in settings such as this one could provide data that better approximate the environments in which human currency systems are at work. Even then, these laboratory or field tests cannot rival what we see in our own species within their economic systems, but those tests would provide new insights into what might be possible for other species to accomplish, and what might not be possible. The goal of comparative research should not be to equate the psychology of human behaviour to that of non-humans (or to divide humans from other species with regard to their psychology), but rather to compare species as fairly as possible. The goal should be to allow comparative data to guide us in understanding how cognition evolves and is constrained or promoted by environmental features as well as the inherent capacities of different species.

Ethics. This article reviews past research and does not include new experimental procedures or new data. All referenced experiments that occurred at the Language Research Center of Georgia State University with non-human primates were conducted under approved protocols of the university's Institutional Animal Care and Use Committee and according to all local and federal guidelines.

Data accessibility. This review article discusses past research and does not include new experimental procedures or new data.

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