Electronic Supplementary Materials

Constructive anthropomorphism: a functional evolutionary approach to the study of human-like cognitive mechanisms in animals

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Notes

Note 1

Note that studies on "state dependent valuation" [1–4] do not yet provide evidence for the representation of the state of hunger in memory. This is because the effect of state on value can also be explained by a simpler mechanism that increases the associative strength of anything learned during the state of hunger. Such simpler mechanisms result in constant preference of the stimulus learned when hungry, a preference that cannot be reversed when in a state of satiation. In fact, in the abovementioned studies of state dependent valuation the level of hunger during the test had no effect on choice, which goes against our prediction of state-dependent learning. This may be interpreted as reflecting a lack of representation of the state of hunger in the tested animals' memory, or alternatively, as a stronger effect of state-dependent valuation that masked the potential effect of state-dependent learning. Studies that are more in line with our reasoning are those in which honeybees' ability to learn to prefer different visual stimuli in different times of the day were taken as evidence for the existence of time representation (a circadian clock, [5,6]), and recent studies in rats showing that an aversive stimulus associated with salt becomes appetitive when the rat was tested in a state of salt deprivation [7,8].

Note 2

Multiple representations of past events in the form of frequency distribution, rather than a single aggregated value, may also be used (e.g. [9,10]). In these cases as well, however, repeated observations are aggregated and reduced into statistics, while the detailed historical data is lost.

Appendix A:

Emotional states and their representations in memory

1. Fear

The reasoning outlined in our discussion of hunger (see main text) can now be applied to other emotional states. The state of fear, for example, is also relatively simple. It has been studied extensively in both animals and humans (e.g. [11–14]) and in relation to its effect on learning [15–18]. It is hardly disputed that animals experience a state of fear that involves a range of behavioural and physiological adjustments that are generally adaptive [11,19]. It is less clear, however, whether animals represent the experience of fear in their memory. The arguments presented for the case of hunger may similarly apply here. Representing the sensory experience of fear in memory should be possible, and having such a representation may be adaptive if it improves state-dependent recall of context appropriate information. For example, if the sound or the image of an approaching predator is learned in association to the state of fear, future encounters with these stimuli would not only trigger fear, but also elicit memories of past encounters, making them available for quick decision making. A young Thompson's gazelle may thus be able to decide whether the cheetahs observed at some distance are of immediate danger, based on the contextual similarity of the current situation to past encounters, where its fear was induced by the behaviour of its mother (who sent alarm signals and fled).

Finally, as discussed above for the state of hunger, having a representation of the state of fear in some animals does not imply that these animals experience fear as humans do. Here again, the human experience of fear may elicit a wider range of associations, including associations with complex representations that are unique to humans. For example, human are able to develop fear of a situation they have never encountered, after hearing about the experience of someone they have never met. The difference, however, is not necessarily in the representation of fear, but in the other representations to which fear can be associated.

2. Jealousy

Let us consider now an advanced emotional state such as jealousy in humans. We will use a basic definition of jealousy, viewing it as an emotion driving goal-directed behaviour aimed at

protecting a social bond; interestingly, the definition cited here specifically associates jealousy with benefits to survival [20]. Scientists usually do not attribute human-like jealousy to animals, and when they do, they carefully refer to it as a primordial version of human jealousy (e.g. [21,22]). Our approach would be to ask whether animals need a state reporting system that is equivalent to Jealousy and whether they represent it in memory.

From a functional viewpoint, we can easily identify circumstances where animals are threatened by competition and should act appropriately. For example, in the case of competition for food among group members, or in the case of male mate guarding (that in humans is clearly associated with the concept of jealousy [23]. In fact, in almost any "zero-sum game" in nature, information about rivals' success or potential success is highly important. Animals tend to respond to such situations by becoming more competitive and aggressive, by defending their resources, or even by attacking potential competitors [22,24]. It is therefore reasonable to assume that animals have a "state reporting system" for competitive situations. Yet, it is not clear whether they have a representation of this state, and how similar is this representation to what we view as jealousy in humans.

We have already suggested that from a mechanistic viewpoint, any state can potentially be represented in memory, but a tendency to preserve this representation in memory should evolve only when it is adaptive. In the case of competitive situations, we believe that the adaptive value of representing the state in memory may be less clear than in the case of hunger or fear. This is because it is not always clear that new information learned during a competitive state should be strongly associated with this particular state, rather than being generalized across different states. For example, noticing another individual finding high quality food items in a new setting may trigger a competitive state in social foragers. Yet, it would be better to remember the features of the new setting, and use them as food-related cues regardless of the presence of competitors. In other words, contrary to our argument in the cases of hunger or fear, state-dependent recall may be counterproductive in this case. It may impair, for example, social learning (e.g.[25]). Accordingly, social foragers may not benefit from representing a state of "jealousy" to which context specific information is associated. The situation may be different, however, in the case of mate guarding, where state-dependent recall can be helpful. For example, a male observing his mate being courted by another male may benefit from associating the image of this particular

male with the representation of the state of "jealousy". This would allow representing this particular male as a specific threat in the context of mate guarding. Consequently, future encounters with this particular male would elicit the state of "jealousy" in the guarding male, making him vigilant, watchful over the female, and perhaps aggressive towards the competitor. This association may also allow the guarding male to learn to recognize behavioural patterns in his mate indicating that she is soliciting another male (e.g. disappearing more frequently than usual – see [26] for relevant description in birds). An ability to identify such patterns and deter competition has an obvious adaptive value, in avoiding mate loss or the possibility of rearing young that are not the guarding male's biological offspring.

Interestingly, this functional evolutionary approach to "jealousy" in animals may also shed new light on the evolutionary roots of jealousy in humans. It suggests that the state of jealousy should be felt most intensely under circumstances in which learning the identity of the competitor, or other contextual details, is helpful in future encounters. Otherwise, there is no need to represent the feeling of jealousy in memory.

As in the case of hunger or fear, we may seek evidence for a representation of a jealousy-like state in animals by using state-dependent learning (i.e. by showing state-dependent recall of items learned under jealousy versus non-jealousy states). But here again, even if such representations exist, it does not mean that animals feel jealousy as humans do; the range and complexity of possible jealousy associations in human – for example, cultural norms regarding fidelity between mates – may not exist in animals.

3. Pair bonding and "being in love"

Let us go back now to the human emotional state of being "in love" and to the example mentioned briefly in the Introduction regarding recent studies on the monogamous prairie vole (e.g. [27–29]). As we claimed earlier, mechanistic similarities at the neuronal or hormonal levels, as well as functional similarities in establishing a pair bond and coordinated parental care, are insufficient to justify the term "love" in the case of prairie voles (or in other non-human animals). Yet, our approach may help to better understand this gap. Following our earlier examples, the first questions to ask is whether the sensory activities experienced in the context of pair bonding behaviour can be represented in memory and what is the adaptive value of

4

representing it. Again, we suggest that constructing a memory representation of this state should be feasible and that the adaptive value of preserving this representation depends on the advantage of state-dependent learning and recall. In the case of pair bonding there are many reasons to believe that state-dependent learning is important. Pair-bonding and pair-activities are clearly developed based on repeated encounters and accumulated experience [30]. Mate recognition must be learned, and there is an advantage in connecting mate representation in memory to the states of pair-bonding or pair activities: this way, seeing the mate would elicit the pair-bonding state and activate the range of memories that are relevant to the context of the pair's activities. Similarly, being in a state of pair-bonding or pair activities would activate memories of the mate (how it looks and smells, where to find it, how it responded in the past to various actions or situations). Thus, there is plenty of learned information that is specific to the context of the pair's behaviours, making state-dependent learning and recall potentially useful.

The arguments above suggest that it is both feasible and adaptive for prairie voles (and for other animals) to have a memory representation of the experience felt while in the state of pair-bonding or pair activities. This state not only triggers physiological and behavioural changes, but may also elicit a range of memories that were associated with this state in the past. What is then the difference between this emotional state in animals, and the feeling of being in love in humans? As discussed earlier for the cases of hunger, fear, and jealousy, the mechanisms of the emotional state may be very similar, but the quantity and the complexity of the representations that can be associated with this state can make a big difference. Humans can obviously associate their pair-bonding state with some highly complex representations of past episodes, shared future plans, and concepts such as "self" and "others" that may not be well represented in animal brains. All these complex memories may give humans' state of "pair bonding" additional dimensions that may not exist in animals, and these define what we commonly view as "being in love" in humans.

Appendix B

Goals, desires, causality and intentionality

Discussions of human decision making and planning may frequently involve terms such as goals, desires, causality, and intentionality, that are difficult to evaluate in the context of animal behaviour (see e.g. [31] for in-depth discussion). Our approach does not provide easy solutions for such problems but may offer a way to think about them. When addressing terms like goals or desires we may ask whether it would be feasible and adaptive for animals to represent them in memory. Our view is that if animals construct an associative network that represents the transitional probabilities between various objects or actions, then, a goal can be any node or section of this network. It can certainly be a food item, or a location from which to access this food item, or a conspecific who should be approached for that purpose. Having the goal represented in the network can clearly help navigate towards it and plan the necessary actions (see e.g. [32,33], for a possible implementation). The second problem is explaining what causes a specific node (or a section) in the network to become a goal, and how a desire for this goal can emerge. Roughly speaking, we suggest that the emotional and physiological states discussed earlier (e.g. hunger, fear, pair-bonding etc.) define the current needs of the animals and activate the relevant representations that are either innate (e.g. food) or acquired (e.g. food-related cues or sets of actions). Viewing goals and desires at this level does not imply that animals "understand" or are "aware" of their goals or desires. In some sense, such an "understanding" may emerge (if at all) from the construction of higher hierarchy in memory that represents the typical sensory experience felt under many instances of having goals and desires (i.e. the sensory experience that is common to many different cases of wanting something). We cannot tell whether animals construct such high order representations. It is conceivable that they can do this because from a computational point of view, the process should not be different from other forms of generalization in which animals represent the concept of "things that can be eaten" or "things that can fly" by their similar link structure (e.g. [32,34]). As for "causality" and "intentionality", our approach does not define them in behavioural criteria (as in [31]), but using a network approach may help demystify such concepts, and describe them in computational terms. Causality may be represented, for example, by a strong directed link (i.e. high transitional probability) from an action to outcome, and intentionality can be the outcome of having a state

that activates a goal represented in the network (see above), in combination with a path in the network representing how a set of actions lead to this goal (which is in line with the suggested interaction between *desire* and *instrumental beliefs* proposed by [31]).

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