Neurobiology of Learning and Memory 125 (2015) 93–97

Contents lists available at ScienceDirect

Neurobiology of Learning and Memory

journal homepage: www.elsevier.com/locate/ynlme

Review

How does the hippocampus shape decisions?

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ARTICLE INFO

Article history:
Received 8 May 2015
Revised 30 July 2015
Accepted 11 August 2015
Available online 19 August 2015

Keywords:
Decision making
Value
Hippocampus

ABSTRACT

Making optimal decisions depends on an appreciation of the value of choices. An important source of information about value comes from memory for prior experience. Such value-based learning has historically been considered the domain of a striatal memory system. However, recent developments suggest that memorial representations supported by the hippocampus may also contribute to decision making. Unlike striatal representations, hippocampal ones are flexible; they can be modified and updated as new information is acquired. In this paper we argue that the hippocampus plays a pivotal role in value-based decision making via three flexible learning mechanisms: (1) updating, (2) generalization, and (3) construction.

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1. Introduction

Under conditions of choice, decisions are often guided by memory for previous experiences and their associated value: Positive experiences are more likely than negative ones to be selected again. The role of memory in guiding choice is well established both in humans and in non-human species. Although memory-guided decision making arguably involves multiple brain systems, research has focused largely on the role of gradual and incremental stimulus–response learning supported by the striatum and other reward-based circuitry (e.g., medial prefrontal cortex; mPFC) in guiding choice. However, recent evidence has suggested that memory processes mediated by the hippocampus may also bias decisions in ways that have not been previously appreciated (also see Delgado & Dickerson, 2012; Shohamy & Turk-Browne, 2013; Wimmer & Shohamy, 2011). Unlike the striatum, the hippocampus supports learning through the rapid acquisition of information following a single exposure. Critically, hippocampal representations are flexible; they can be modified and updated as new information is acquired. The flexible nature of hippocampal computations not only serves memory, but also supports the novel representation of future experiences (Schacter & Addis, 2009), making the hippocampus particularly well suited to support decision making. In this paper we argue that the hippocampus uniquely biases value-based decision making processes via three flexible learning mechanisms: (1) updating, (2) generalization, and (3) construction. We also briefly consider whether the contribution of the hippocampus to decision making extends beyond its role in creating novel flexible representations and conclude that although there is accumulating evidence that the hippocampus is sensitive to stimulus value, there is insufficient support for the notion that the hippocampus computes value per se.

2. Updating

The first way in which the hippocampus may support value-based decisions is by updating the value representation of previously learned information. This "updating" hypothesis was initially put forth to account for the observation that hippocampal damage impairs value-based decision making on a gambling task that models real-life decisions (Iowa Gambling Task; Gupta et al., 2009; Gutbrod et al., 2006; also see Rubin, Watson, Duff, & Cohen, 2014). In the Iowa Gambling Task, participants repeatedly select from four decks of cards. Two of these decks yield small rewards and even smaller punishments overall ("good" decks), while the remaining two decks yield large rewards but even larger punishments overall, and are thus unfavorable over the long term ("bad" decks; Bechara, Damasio, Damasio, & Anderson, 1994). Damage to the hippocampus results in no preference between good and bad decks (Gupta et al., 2009; Gutbrod et al., 2006) as patients tend to be responsive only to the most immediate outcome (i.e., favoring an alternative deck when the most recent deck yielded punishment, rather than tracking gain over the long term). The involvement of the hippocampus in this task was somewhat unex-

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http://dx.doi.org/10.1016/j.nlm.2015.08.005
1074-7427/Published by Elsevier Inc.

pected because, historically, the prevailing view had been that the hippocampus is not necessary to support basic stimulus–response learning that the Iowa Gambling Task appears to draw on. Yet, the necessity of the hippocampus for performance on this task may be due to the greater demands on flexible updating relative to other feedback-based tasks that involve the acquisition of stimulus–response outcomes (i.e., learning to repeat previously reinforced behaviors), for which patients with hippocampal damage are unimpaired (e.g., Foerde, Race, Verfaellie, & Shohamy, 2013; Knowlton, Squire, & Gluck, 1994). More specifically, a key feature of the Iowa Gambling Task is that it requires not only tracking reward information for each deck, but updating the comparative value among decks based on the incorporation of occasional loss information within each deck (e.g., Deck C is more valuable than Deck B; Gupta et al., 2009). Accordingly, the suggested role of the hippocampus is to update the value as learning unfolds, i.e., across trials. Converging evidence for this conclusion comes from a functional imaging study that implicates the hippocampus in value-based decisions that involve flexible updating of responses and reward outcomes across trials (Guitart-Masip et al., 2013).

Whereas the foregoing findings suggest a role of the hippocampus in updating information *across* trials, it is conceivable that the flexibility afforded by the hippocampus may also be critical in situations where updating is required *within* a trial. For example, a faulty updating mechanism may account for the altered performance of hippocampal-lesioned rats on another sort of decision-making task, namely, one that requires intertemporal choices. In a typical intertemporal choice paradigm, rodents are required to choose between two food rewards: a smaller one available immediately and a larger reward that is received after a delay (typically 10 s). Several studies have shown that, relative to control rats, hippocampal-lesioned rats show a greater preference for the smaller, immediate reward (Cheung & Cardinal, 2005; Mariano et al., 2009; McHugh, Campbell, Taylor, Rawlins, & Bannerman, 2008; Rawlins, Feldon, & Butt, 1985). Despite the consistency of this finding in the literature, the mechanism underlying this impairment remains unknown. One possible explanation for this result is that hippocampal lesions impair updating of the value of the delayed option: In control rats, the degradation in value produced by the aversive nature of the delay (which is experienced first) is partially overridden by the size of the subsequently-received reward (i.e., the initial value computed based on the delay gets updated to include information about the reward magnitude). By contrast, in hippocampal-lesioned rats, this value updating may be deficient such that choice is driven primarily by the aversive nature of the delay. Future research is necessary to test this hypothesis directly. Notably, the observed impairment in intertemporal choice cannot be accounted for by a more basic learning deficit as hippocampal-lesioned rats can learn to choose the larger reward when both options are delayed. Because learning in this condition is based on a single contingency (i.e., magnitude of reward) it does not require updating of value, as is the case in standard intertemporal choice where both magnitude of the reward and delay are relevant.

Intriguingly, in stark contrast to rodent studies, standard intertemporal choice in humans does not seem to involve the hippocampus (but see "construction" section below): Patients with amnesia who have damage to medial temporal lobe structures (including the hippocampus) show intact intertemporal choice performance, albeit using more restricted quantitative outcome measures relative to the larger literature (Kwan, Craver, Green, Myerson, & Rosenbaum, 2013; Kwan et al., 2012, 2015; Palombo, Keane, & Verfaellie, 2015b). Importantly, many human analogues of intertemporal choice involve only secondary reinforcers (e.g., money). Regardless of whether such rewards are real or hypothetical, in most cases they do not require the individual to experience either the delay or the consumption of the reward in real time and thus may not require reward-updating mechanisms supported by the hippocampus.

To date, arguments favoring the involvement of the hippocampus in updating reward value have come almost exclusively from post hoc interpretations of experimental findings rather than from experiments designed explicitly to test this hypothesis. Limited research that has specifically examined the involvement of the hippocampus in updating does not consider the possible contribution of basic learning (rather than updating) mechanisms to account for decision making deficits following hippocampal damage (De Saint Blanquat, Hok, Save, Poucet, & Chaillan, 2013). A strong test of the hypothesized role of the hippocampus in value updating, both within and across trials, would require a comparison of decisions under conditions designed to differ specifically and exclusively in their demand on updating.

3. Generalization

In addition to its role in biasing choices through updating, the hippocampus may also support decision making by generalizing value across related experiences. Much of the evidence for this notion comes from studies involving transfer of value, a line of research pioneered by Wimmer, Shohamy, and colleagues (e.g., Gerraty, Davidow, Wimmer, Kahn, & Shohamy, 2014; Wimmer & Shohamy, 2012). Under conditions where two stimuli are associated (preconditioning; pairing of item A with item B), subsequent Pavlovian conditioning of one member of the pair (item A) with a monetary reward can enhance choice of the second (non-rewarded) member (item B) during a subsequent decision phase (i.e., transfer of value; see Fig. 1 for a schematic of a typical transfer of value paradigm). Critically, the magnitude of this value transfer effect (i.e., the proportion of trials on which the associate of the rewarded item is selected [item B] over an associate of a non-

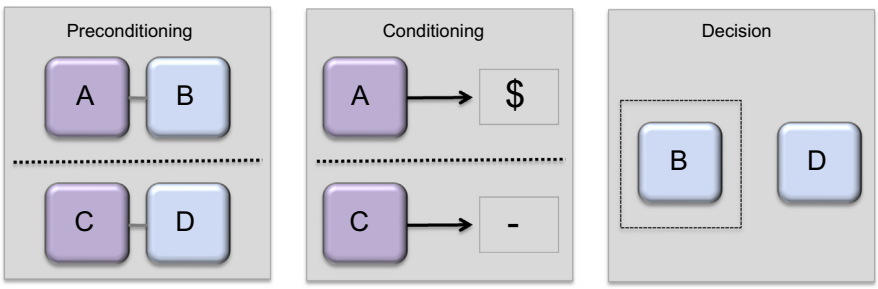

Fig. 1. Depiction of a typical transfer of value paradigm. As described in the text, transfer of value typically involves three phases: preconditioning (associative learning), conditioning (reward learning) and a decision, as in Wimmer and Shohamy (2012). Note that the associative and reward learning phases can also be presented in reverse order, as in Gilboa et al. (2014).

rewarded item [item D]) is predicted by the strength of hippocampal activity and hippocampal-striatal connectivity across participants (Wimmer & Shohamy, 2012), despite no explicit awareness of this transfer.

What is the precise cognitive mechanism of hippocampal involvement in supporting generalization (transfer of value) under such circumstances? An obvious candidate is a retrieval-based one, whereby hippocampally-mediated transfer occurs "on the fly" at the moment of decision (such that the selection of an associate of the rewarded item is driven by retrieval of its link to the rewarded item); under some circumstances transfer of value indeed occurs at retrieval, as the magnitude of transfer of value is associated with activity in the hippocampus during a decision phase (Bornstein & Daw, 2013; Kahnt, Park, Burke, & Tobler, 2012).

Interestingly, Wimmer and Shohamy (2012) demonstrate a circumstance in which hippocampal-mediated transfer can occur even earlier, during encoding of a reward association: In their study, the magnitude of transfer of value in the subsequent decision phase was correlated with hippocampal activity and connectivity that occurred during the Pavlovian conditioning phase (i.e., when A was paired with a reward) but was not associated with activation either in the hippocampus or elsewhere in the brain during the subsequent decision phase (i.e., when a decision regarding B was made). A similar "encoding" mechanism has been demonstrated during associative inference whereby the inference of A–C following the encoding of premise pairs A–B and B–C is associated with hippocampal activation during the encoding of B–C (e.g., Zeithamova, Dominick, & Preston, 2012). The results of Wimmer and Shohamy (2012) are unique, however, in suggesting that the role of the hippocampus in generalization extends to value-based learning even though learning of such value-based associations is in itself not hippocampally dependent. The generalization of value is likely adaptive in many ways as it provides a heuristic for judging novel experiences: Our impulse to extend a lunch invitation to a new neighbor may be biased by a prior pleasant experience with the neighbor's spouse.

In determining the scope of hippocampal involvement in transfer of value, an important question for future research is whether the hippocampus supports transfer even when the initial learning of the information that enables transfer (i.e. the preconditioning phase in Wimmer & Shohamy, 2012) does not require the hippocampus. That is, it is possible that in their study, learning during the preconditioning phase, when the A–B pairing was first established, was dependent on hippocampally-mediated associative mechanisms. As such, hippocampal involvement in transfer of value might be a consequence of the fact that subsequently reactivating the second member of the pair during the reward phase requires the hippocampus. Intriguingly, Gilboa, Sekeres, Moscovitch, and Winocur (2014) recently investigated the role of the hippocampus in transfer of value (using a lesion approach), except the learning phases were reversed in comparison to Wimmer and Shohamy (2012) such that the initial learning phase (i.e., Phase 1) involved non-hippocampal processes: In their study, rats were trained to associate a tone (i.e., tone A) with a food reward (presumably a striatally-mediated form of learning). In Phase 2, the same tone was presented with a novel tone (i.e., tone B). Following this associative pairing phase, intact rats demonstrated, as expected, both first and second order conditioned responses to A and B, respectively. In other words, intact rats associated A with a reward, and also demonstrated a transfer of value from A to B such that B inherited the reward contingency of A. However, rats with hippocampal lesions only demonstrated the conditioned response to A (learned in Phase 1) but did not transfer value. These results provide evidence that the hippocampus can be required for value transfer even when it is not necessary for the acquisition of the initial information that enables transfer.

Given that Phase 1 in Gilboa et al. (2014) involved non-hippocampally mediated value-based learning, a question that remains unanswered is how the hippocampus has access to these value representations to support subsequent transfer in intact rats. One possibility is that during initial reward learning, the hippocampus, while not required for task performance per se, nonetheless establishes a redundant representation of, e.g., striatally-mediated stimulus reward contingencies. This hippocampal representation is a "just in case" mechanism as it serves future choice when needed. Consistent with this notion is the observation that the hippocampus is active during simple reward learning, even though it has been demonstrated to be unnecessary for performance (e.g., see Gluck, Ermita, Oliver, & Myers, 1997 for review). More direct support for this view would come from an imaging analogue of the Gilboa et al. (2014) study, demonstrating that the extent to which the hippocampus tracks reward information during initial acquisition of value-based associations is in fact related to subsequent value transfer.

4. Construction

A third way in which the hippocampus may support value-based decision making is by constructing a novel representation based on an extrapolation from previous experiences. Support for this idea comes from an elegant set of experiments by Barron, Dolan, and Behrens (2013) in which individuals had to construct the value of novel goods with which they had no prior experience. In an initial experiment, participants were asked to make choices between two novel compounds, where each compound (e.g., raspberry avocado smoothie; AB) was comprised of two familiar component foods (raspberry, A; avocado, B). Activation in the mPFC during compound choices was correlated with subsequent valuation of the compounds measured offline. Based on the observed relationship between brain activity and later valuation, the authors next asked: How does the brain construct the value of the novel compounds? To address this question, they conducted an experiment in which they took advantage of the well-known phenomenon of repetition suppression (i.e., attenuated activation when a familiar item is repeated over a short interval). During scanning, participants were simply asked to imagine AB compounds, but prior to imagining AB compounds, subjects imagined either A or B in isolation. A control trial consisted of imagining an unrelated food (item C) prior to imagining AB. Repetition suppression occurred in both the hippocampus and mPFC during imagining AB, when preceded by A or B (but not C) suggesting that AB representations are the product of imagining the individual A and B representations in isolation. Together, these findings suggest that while the mPFC may be involved in novel value computation (suggested by virtue of the observed correlation between mPFC activity and subsequent valuation), the hippocampus, in addition to the mPFC, may play a role in the initial generation of novel experiences, thus contributing necessary "input" for value assignment.

Additional evidence for the role of hippocampally-mediated construction processes in value-based decision making comes from studies investigating temporal discounting (the well-documented tendency for humans to devalue a reward to account for its delay in arrival). As noted earlier, the hippocampus is not required for standard intertemporal choice in humans: Amnesic patients with medial temporal lobe damage do not differ from healthy controls in the extent to which they discount the future (Kwan et al., 2012, 2013, 2015; Palombo et al., 2015b), and functional neuroimaging studies do not show evidence of hippocampal involvement in standard intertemporal choice (e.g., Peters & Büchel, 2009). However, there is another version of intertemporal choice that involves "baiting" the future choice with an episodic event.

In this version, participants are asked to construct an imaginary event (i.e., episodic future thinking) involving consuming the future reward within the context of a scenario prior to making their intertemporal choice (e.g., imagine spending $40 at a pub in 2 months; Benoit, Gilbert, & Burgess, 2011; Kwan et al., 2015; Lin & Epstein, 2014; Liu, Feng, Chen, & Li, 2013; Palombo et al., 2015b; Peters & Büchel, 2010). Previous research shows that temporal discounting is attenuated (i.e., individuals are more willing to wait for the later, larger reward) when participants are asked to engage in episodic future thinking. Critically, this attenuation involves the hippocampus: Functional neuroimaging data demonstrates that the magnitude of this attenuation is correlated with hippocampal-neocortical coupling (particularly with midline prefrontal regions; Benoit et al., 2011; Peters & Büchel, 2010). Moreover, the necessity of the hippocampus is demonstrated by a recent study from our laboratory showing that amnesic patients with medial temporal lobe lesions (who are profoundly impaired in episodic-future thinking; see Race, Keane, & Verfaellie, 2011) do not show attenuated discounting following instruction to engage in episodic future thinking (Palombo et al., 2015b), whereas they show intact performance on a standard intertemporal task that does not draw on episodic future thinking (but see Kwan et al., 2015; also see Palombo, Keane, & Verfaellie, 2015a for discussion).

Perhaps analogous to the notion of future thinking in humans is the phenomenon of "preplay" in rodents: When faced with a choice of which arm to enter in a T-maze, rats engage in "vicarious trial and error" (VTE, consisting of small head movements that alternate between options) before coming to a behavioral choice. VTEs are thought to be hippocampally-mediated: During VTE, anticipatory forward shifting neural representations of space are observed in the hippocampus (in area CA_3), moving first within the neural ensembles that represent one arm and then the next arm (Johnson & Redish, 2007), and hippocampal lesions disrupt VTE behavior (Hu & Amsel, 1995). This type of forward shift (or preplay) is thought to be a neural mechanism for consideration of choice in rodents.

Kurth-Nelson, Bickel, & Redish (2012) argue that this type of vicarious sampling may be adaptive in that it may help in determining the subjective value of a future reward. Together, these studies hint at an adaptive function of hippocampally-mediated constructive processes (Boyer, 2008). By building new representations, extrapolated from the sum of prior experiences and their associated value, we are able to represent hypothetical choices and their worth without actually experiencing these choices – an intrinsic *look before you leap* (Palombo et al., 2015a).

5. Beyond flexible processes: Does the hippocampus compute value?

The preceding sections suggest that the hippocampus supports value-based decision making via three proposed flexible learning mechanisms—updating, generalization, and construction. What these processes have in common is that they involve the flexible leveraging of memorial information to serve future choice. In order to support these processes, the hippocampus obviously requires access to information about value. An important question for future research is to determine precisely what mechanisms provide the hippocampus with such value information "just in case" it is needed (as discussed earlier). One possibility is that the initial computation of value is accomplished in other brain regions but that these signals are forwarded to the hippocampus so that this information can facilitate learning (Adcock, Thangavel, Whitfield-Gabrieli, Knutson, & Gabrieli, 2006) and future-oriented decisions. The transmission of value-based information may be supported by interactions between the hippocampus and the striatum (Kahn & Shohamy, 2013; Ross, Sherrill, & Stern, 2011; Wimmer & Shohamy, 2012). Still in other cases, this transmission may be mediated by coupling between the hippocampus and mPFC (Barron et al., 2013; Benoit et al., 2011; Peters & Büchel, 2010). It will be important to determine under what conditions the hippocampus interacts with striatal regions versus mPFC regions.

An alternative possibility is that the hippocampus plays a more *direct* role in processing reward information by actually computing value signals "in house." In rodents and primates, hippocampal neurons are modulated by reward outcomes, firing more robustly for rewarded than unrewarded trials (e.g., Holscher, Jacob, & Mallot, 2003; Rolls & Xiang, 2005), and recent preliminary evidence from rodents suggests not only that neurons in the hippocampus (particularly area CA_1) are responsive to expected and observed reward value, but that these value-based hippocampal signals are highly similar to those observed in striatal and prefrontal regions (see Lee, Ghim, Kim, Lee, & Jung, 2012). These findings have been interpreted as reflecting a direct role of the hippocampus in coding value. However, although these studies suggest that the hippocampus is indeed sensitive to information about value, whether the hippocampus actually computes value signals independent of those computed by the striatum and other regions still needs to be determined, as only this type of evidence would demonstrate that value computation takes place in the hippocampus per se. More broadly, there is much to be learned about the role of the hippocampus in biasing value-based decision making; the studies described here provide a fertile ground for exploring this topic further.

Acknowledgments

D.J.P is supported by the Canadian Institutes of Health Research. M.V. is supported by the Department of Veterans Affairs Clinical Science Research and Development Service. The authors declare no conflicts of interest. The contents of this manuscript do not represent the views of the U.S. Department of Veterans Affairs or the United States Government.

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