Neuroscience and Biobehavioral Reviews 79 (2017) 48–65

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

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

Review article

The neural basis of delay discounting: A review and preliminary model

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A R T I C L E I N F O

Keywords:
Delay discounting
Temporal discounting
Impulsive choice
Human
Animal
Neural model

A B S T R A C T

The phenomenology of delay discounting (e.g. shape of the discount function; relation to mental health) has been reviewed in detail previously, but not its neural substrates. Its neuropsychology is crucial for both theory and clinical practice. So, here, we review the neural underpinnings of delay discounting. We introduce its objective summary measures; provide an atheoretical summary of current findings – linking brain regions to each objectively measurable variable; and then provide a preliminary five-stage summary model of cognitive processing; followed by a mapping of parameters to the flow of information through neural systems. The whole is designed to stimulate future research on the roles of each brain region in delay discounting. Delay and payoff produce activity in many brain areas: thalamus; sensory, parietal, temporal, cingulate, prefrontal, motor, and insular cortex; and basal ganglia. Delay discounting, then, appears to emerge from the interaction of neural systems as they process streams of events in recurrent loops and not to be a simple calculation carried out in a single center in the brain.

1. Introduction

Animals, especially the longer-lived ones, are frequently faced with situations where they have to make the choice between an immediate gain and a delayed (particularly larger) gain. For example, in a hunter-gatherer society, a given group of humans may be faced with the choice of spending either a brief time on hunting a small animal or a longer time trying to hunt down a larger animal. Such decisions place considerable demand on the animal's cognitive capacity (O'Connell and Hofmann, 2012): at the least, the decisions require the ability to mentally represent future gains and calculate utility based on such variables as the gains' magnitudes and their associated delays. By extension, the ability to adaptively select pursuit of delayed gains is a testament to the ability of an animal's highly complex brain to process information and predict the future.

It is well established that delay in obtaining a gain reduces its subjective value. For example, a choice between $50 immediately received and $100 to be received after a week may be treated as comparable to a choice between an immediate $50 and, say, an immediate $25. The immediate value that is equivalent to a delayed $100 varies with each person's degree of discounting (e.g., Odum, 2011a). The process through which a perceived gain loses its subjective value as a result of delay is termed 'delay discounting' or 'temporal discounting'. The delay discounting framework allows for the interpretation of a wide range of behaviors across species; and has been of interest to fields as various as clinical psychology (De Wit, 2009), economics (Angeletos et al., 2001), and behavioral ecology (Vanderveldt et al., 2016). Delay discounting also relates to other forms of gain discounting, such as probability discounting (discounting of gains that are less certain compared to certain gains; Green et al., 2014) and effort discounting (the discounting of gains that require greater effort; Prevost et al., 2010).

The phylogenetic and situational ubiquity of delay discounting suggests it is functional; and some degree of delay discounting should be evolutionarily adaptive since delay implies uncertainty, including of loss and possible exposure to threat, and thus reduced utility. However, an excessive rate of delay discounting (i.e. preference for immediate payoffs) appears to make a major contribution to many mental disorders, particularly those on the externalizing spectrum, such as addiction (De Wit, 2009) and ADHD (Barkley et al., 2001). Delay discounting is also greater in adolescents than adults (Christakou et al., 2011). Interestingly, a sudden increase in the rate of discounting generally accompanies relapse (Heather, 1998). A better understanding of the neural underpinnings of delay discounting therefore has implications that are both practical (e.g., for developing psychiatric treatments) and theoretical (e.g., for understanding gain-processing in general).

Most reviews of delay discounting have focussed on phenomenology rather than neural processing (Koffarnus et al., 2013; Vanderveldt et al., 2016). There has only been one brief theory-driven neural review (Peters and Buchel, 2011). Here, therefore, we detail the neural substrates engaged by the delay discounting task. Our goal is to provide

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http://dx.doi.org/10.1016/j.neubiorev.2017.04.022
Received 11 February 2017; Received in revised form 20 April 2017; Accepted 21 April 2017
Available online 29 April 2017
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an atheoretical overview of the extant literature on the neural substrates of delay discounting, and to derive from this a summary neural model as a basis for future research.

This paper is divided into three main sections. First, we assess the term ‘delay discounting’: discussing its conceptual definition; describing how it is operationalized in delay discounting research; and linking faulty delay discounting to clinical disorders, which highlights the practical implications of delay discounting research. Second, we review the extant research on the neural basis of delay discounting to provide a data-driven summary of the literature with no attempt to relate this to any theory until much later in the text. The main text is organized in terms of objectively measurable performance variables. To aid cross-referencing, our tables of the data are organized mainly in terms of brain lobes attempting to keep adjacent structures together. Lastly, based on the review, we formulate a prototype model of the neural systems involved – a first step to a neural theory of delay discounting – and use it to point to future neural research on delay discounting.

2. Delay discounting – definition, theory, and the clinic

2.1. Delay discounting defined

It is thought that, when presented with a possible gain, animals apply a nominal internal exchange rate in some way to mentally represent the subjective value of the gain in a common neural ‘currency’ that allows direct comparison with other potential gains of qualitatively different types (Salzman and Fusi, 2010). The higher this subjective value, the more likely the animal is to pursue the gain. At the operational level, delay discounting is primarily defined by the observed rate of discounting: the rate at which, as demonstrated by behavior, the effective value of a fixed gain declines with increasing post-choice delay of gain delivery. The exact shape of the delay discounting function (and so what is taken to be the ‘rate’) is discussed below and has been an issue of much debate (for a recent review, see Vanderveldt et al., 2016). At the conceptual level, the term ‘delay discounting’ refers to a decline in subjective value with expected delay. While it is possible that the observed behavioral decline could be due to a fixed internal gain value being counteracted by a delay-related internal loss (such as discomfort resulting from waiting), in presenting our model we will also give arguments against this as a primary explanation of discounting – and present discounting as closer to a reduction in positive emotional salience over perceived distance of mental time traveling. On this view, the shape of the discounting function reflects the scaling of the time distance not the interaction of gain and time-varying potential loss.

A typical delay discounting experiment begins by presenting the participant with a choice (either real or hypothetical, with the latter used only for human participants) between an immediate gain and a delayed gain of greater magnitude. A procedure of adjusting the reward values trial-by-trial follows (e.g., Du et al., 2002): If the participant chooses the immediate gain in a trial, the value of the immediate gain in the next trial is decreased; while if the participant chooses the delayed gain in a trial, the value of the immediate gain in the next trial is increased. The size of the adjustment decreases with the number of trials. The subjective value of the delayed gain is then calculated as the midpoint between the last amount of the immediate gain chosen over the delayed alternative and the last amount of the immediate gain rejected. This procedure, if repeated several times with varying magnitudes of delay, produces a number of points through which a ‘discounting curve’ can be drawn for each participant (Odum, 2011b). The discounting curve can be assessed with two alternative classes of metric: (1) the Area Under the Curve (AUC; Myerson et al., 2001), a simple empirical measure; or (2) the discount constant k (Odum, 2011a), which assumes a specific underlying decay function (usually hyperbolic, see below). Both AUC and k are taken to reflect the underlying internal rate of delay discounting, and can be measured as

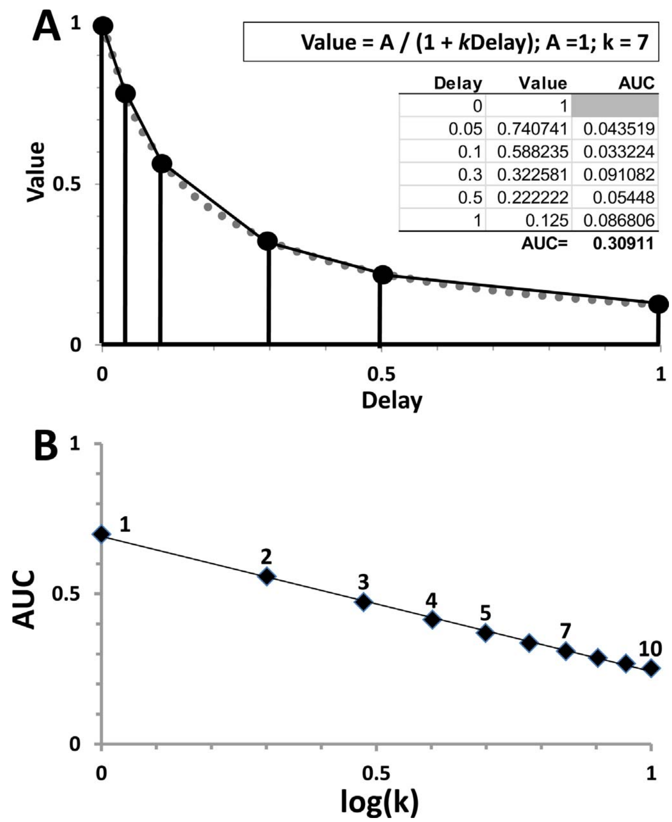

Fig. 1. An example of calculation of AUC and comparison with log(k). (A) The dotted line represents the theoretical underlying hyperboloid function, in this case using the fitting equation of Odum (2011b) with $A = 1$ and $k = 7$. Data points on the curve are placed at the intervals normally used in delay discounting experiments (as in e.g. Myerson et al., 2001) with straight lines showing the boundaries used by the AUC calculation. The inset table shows the AUC component calculated in XL for each trapezoid as ((delay2 − delay1) × (value2 + value1)/2). These values are then summed to produce the final AUC parameter. (B) The values of AUC for $A = 1$ and varying k are plotted against $\log_{10}(k)$ and fitted with a least squares linear regression. It can be seen that AUC and log(k) are in close agreement when the spacing of delays is that shown by the points in panel A.

state (i.e., showing within-person variability over time) or trait (i.e., showing within-person stability and between-person variability; Madden and Bickel, 2010).

To obtain AUC (Myerson et al., 2001), no modeling of the empirical data is needed. Instead, the subjective value of the gain (as the y-axis) is plotted against the gain's delay (as the x-axis). Vertical lines are then drawn from each data point to the x-axis, a procedure that subdivides the graph into a series of trapezoids. The area of each trapezoid equals $((x_2 - x_1) * (y_1 + y_2)/2)$, where x_1 and x_2 are successive delays and y_1 and y_2 are the corresponding subjective values. The AUC for each individual participant is the total area of the trapezoids of his/her discounting curve and its obtained value will vary somewhat with the delay intervals chosen for testing. The smaller the AUC, the more the participant discounts the delayed gain. An example of AUC calculation is shown in Fig. 1.

In the case of k, the discounting curve is usually modeled as a hyperbolic or exponential function, with recent research favoring the hyperbolic, given its better fit to the data (e.g., Odum, 2011a). More recent researchers have also proposed that hyperboloid functions should be used, with nonhuman animals represented best by a hyperboloid with denominator power 1 (which is essentially a hyperbolic curve), and humans represented best by a hyperboloid with denominator power less than 1 (Vanderveldt et al., 2016). Odum (2011b) modeled the participant's rate of delay discounting using the following equation, which provides an estimate of k, after which k or log(k) can be used in analysis:

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