

Economic Choice as an Untangling of Options into Actions

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We propose that economic choice can be understood as a gradual transformation from a domain of options to one of the actions. We draw an analogy with the idea of untangling information in the form vision system and propose that form vision and economic choice may be two aspects of a larger process that sculpts actions based on sensory inputs. From this viewpoint, choice results from the accumulated effect of repetitions of simple computations. These may consist primarily of relative valuations (evaluations relative to the value of rejection, perhaps in a manner akin to divisive normalization) applied to individual offers. With regard to economic choice, cortical brain regions differ primarily in their position and in what information they prioritize, and do not—with a few exceptions—have categorically distinct roles. Each region's specific contribution is determined largely by its inputs; thus, understanding connectivity is crucial for understanding choice. This view suggests that there is no single site of choice, that there is no meaningful distinction between pre- and post-decisionality, and that there is no explicit representation of value in the brain.

Introduction

Many approaches to delineating the neural basis of economic choice begin by identifying the major brain structures that implement it (e.g., [Rangel and Hare, 2010](#); [Rushworth et al., 2011](#); [Figure 1](#)). The list of relevant structures includes the medial and orbital surfaces of the frontal lobes and the ventral striatum, among others ([Bartra et al., 2013](#); [Haber and Behrens, 2014](#); [Heilbronner and Hayden, 2016](#); [Levy and Glimcher, 2012](#); [Padoa-Schioppa, 2011](#); [Rushworth et al., 2011](#)). Single neuron and hemodynamic responses in these regions encode the values of offers and outcomes and track comparisons. Lesion studies confirm that at least some of these regions have a direct causal role in choice (e.g., [Camille et al., 2011](#); [Fellows and Farah, 2005](#); [Noonan et al., 2010](#)).

The regions of the reward system are clearly not the same. They have different cytoarchitecture and different connectivity ([Haber and Behrens, 2014](#); [Passingham and Wise, 2012](#); [Passingham et al., 2002](#); [Petrides et al., 2012](#)). They have distinct functions, as shown by electrophysiological and neuroimaging studies. The functional differences between the regions are also clear from lesion studies (e.g., [Fellows, 2004](#); [Rudebeck and Murray, 2014](#); [Rushworth et al., 2011](#)). But this does not mean they have categorically specialized functions in all domains.

In typical taxonomies, the steps of economic choice involve assigning a value to options, comparing values, selecting the most valued one, and preparing and executing the action associated with the chosen option. The modular approach to functional neuroanatomy of economic choice reifies these steps of choice in the regional architecture of the brain ([Kable and Glimcher, 2009](#); [Padoa-Schioppa, 2011](#); [Rangel and Hare, 2010](#); [Rangel et al., 2008](#)).

Modular models assuming an overt representation are often elaborations on a basic two-stage model. The “pure value”

stage is one in which values are represented in an abstract and domain-independent (that is, amodal) manner ([Landreth and Bickle, 2008](#); [Levy and Glimcher, 2012](#); [Montague and Berns, 2002](#); [Padoa-Schioppa, 2011](#)). This pure value stage has the presumed benefit of allowing comparison of dissimilar goods. Given a pure value stage, a brain region can be classified as pre-decisional (if its computations occur before choice) or post-decisional (if they occur afterward; [Blanchard and Hayden, 2014](#); [Cai and Padoa-Schioppa, 2012](#); [Rangel and Hare, 2010](#)). The second stage is an action selection stage, at which the results of the comparison are transformed into appropriate actions ([Chen and Stuphorn, 2015](#); [Hare et al., 2011](#); [Wunderlich et al., 2009](#)).

In contrast, the untangling approach, which we propose and delineate here, sees the choice as a relatively smooth transition from an input to an output space. Each region performs non-linear operations on its inputs and converts them into a format more amenable to threshold-based decision-making (which can only occur on fully untangled representations). In this view, regions differ, for the most part, quantitatively, but not qualitatively—at least in the domain of choice. They may and likely do have categorically different functions in a domain other than choice.

Of course, different brain regions likely evolved at different times and have special roles in particular evolved behaviors ([Murray et al., 2014](#); [Passingham and Wise, 2012](#)). They may even compute separate and unrelated, or possibly competing, forms of value ([Rushworth et al., 2012](#); [Murray et al., 2014](#)). Nonetheless, when performing simple economic choices, we propose that they may be part of a larger whole with a more general single role.

The untangling view is serial and hierarchical ([Cisek, 2012](#); [Cisek and Pastor-Bernier, 2014](#); [Hunt and Hayden, 2017](#)). That is, some regions sit at an early stage that is more input-like



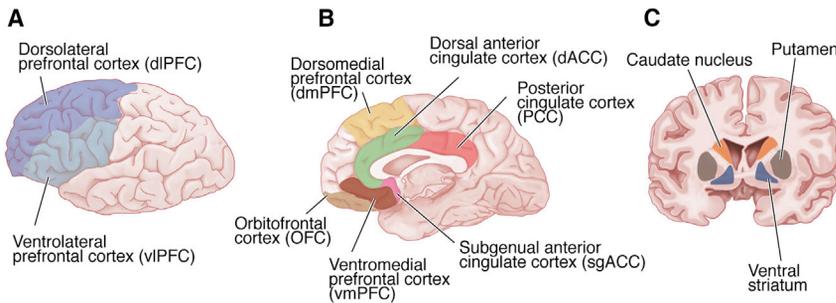


Figure 1. Some of the Brain Regions Associated with Economic Decision Making
Figure from *Neuroscience* (6th edition) by Purves et al. (2017).

(and carry more details about sensory, visceral, and other inputs) and other regions sit at a late stage that is more output-like (and have more details about motor commands). Early, middle, and late stages all participate in gradually transforming input information to action. There is no pure value stage—just a middle stage with both input- and output-like aspects (Balasubramani et al., 2018). Critically, that middle stage is not a pure value stage in any of the senses that that term is used—it’s just part of the way along the untangling process.

To be a bit more specific, we propose that the organization of regions is not linear but dendriform. Action depends on the integration of multiple distinct inputs, which converge at multiple points, toward a final common pathway in the motor system. These input regions may have specialized content, but they shape that information so that it can be integrated into the gradually evolving decision process.

The Analogy with the Form Vision System

To help us understand the functional anatomy of the reward system, we find it useful to think about the organization of the form vision system (Figure 2). The arrangement of visual areas spanning the occipital pole (caudally) to the temporal pole (rostrally) is organized roughly in a series (Logothetis and Sheinberg, 1996; Tanaka, 1996), albeit with many exceptions (Felleman and Van Essen, 1991).

One historically important debate centered on the question of modularity. The modular argument was that individual visual areas are specialized for particular gestalt aspects of form (Zeki, 1978). For example, V1 for orientations, V2 for texture (or figure-ground segmentation), MT for motion, and V4 for color. In this view, regions had categorically distinct functions. In the alternative view, each region corresponds to a particular stage of constructing an abstract representation of a complex form (or, more broadly, in a sensorimotor transformation; Maunsell and Van Essen, 1983).

For example, early work suggested that V4 was specialized for color (Zeki, 1978). Subsequent work indicated that V4’s role in color processing is not very different from those of adjacent areas (Maunsell and Van Essen, 1983; Motter, 1994; Schein et al., 1982). These regions also have color selectivity and V4 has form selectivity, and its form selectivity is an intermediate type between what is observed in its afferent V2 and its efferent PIT (David et al., 2008; Desimone and Schein, 1987; Mazer and Gallant, 2003; Yamins et al., 2014). Nor are these properties limited to form processing. For example, V4 shows evidence

for attentional selectivity, in weaker form than later regions, and in stronger form than earlier ones (Luck et al., 1997) and executive functions like working memory, decision, and salience (Hayden and Gallant, 2013; Mazer and Gallant, 2003; Mirabella et al., 2007; Ogawa and Komatsu, 2004).

This does not mean that we are simply looking in the wrong place for color vision when we look at V4. Color vision is not localized to a single brain region; it is distributed. Early regions and later regions differ in how they represent it.

Untangling Information in Form Vision

The form vision system offers an example of how repeated simple computations can, when organized serially and hierarchically, lead to nonlinear computations. When information passes from one region to the next, it is untangled (DiCarlo and Cox, 2007; DiCarlo et al., 2012; Pagan et al., 2013; Tafazoli et al., 2017). In other words, the information is preserved in an information-theoretic sense, but its format is transformed so that it is more readily decodable. This transformation facilitates linear decoding (Figure 3).

A great deal of important information is present on the retina (direction, color, form, etc.), but not in a format that is useful. One of the major roles of the visual cortex is transforming the retinal representation into one that is linearly decodable by downstream regions. When the information is fully untangled, then a linear hyperplane (which can be implemented by single neurons) will suffice to serve as a category boundary and implement a decision (DiCarlo and Cox, 2007; DiCarlo et al., 2012; Hung et al., 2005).

Decoding can also involve combining across dimensions. For example, Pagan and colleagues recorded responses of neurons in the inferotemporal cortex (IT) and perirhinal cortex (PRH) in a delayed match to sample task (Pagan et al., 2013; Suzuki and Amaral, 1994). PRH is positioned later in the hierarchy than IT (Suzuki and Amaral, 1994). Both regions share the same information and the amount of task-relevant information was equal in both regions. But that information is untangled—more linearly decodable—in PRH than in IT (Pagan et al., 2013). Critically, their task did not just require processing of form; subjects had to compare stimuli to information stored in working memory. Thus, the complete untangling process involved integrating two independent information streams.

To make an economic choice, we must also untangle information. This process includes object identification (“is that gazelle wounded or healthy?”) and subsequent steps leading to action (“what speed and direction should I run to catch the gazelle?”). During this process, all relevant information must be transformed into a format such that motor thresholding processes are sufficient to implement the choice (Cisek and Pastor-Bernier, 2014; Pezzulo and Cisek, 2016).

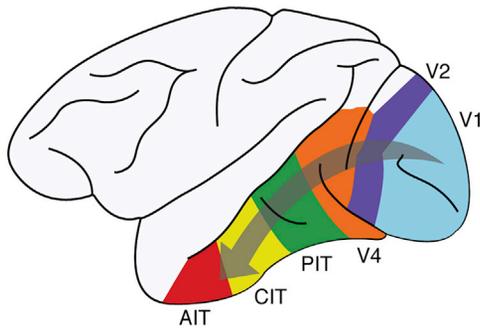


Figure 2. Cartoon of the Form Vision Pathway

Input from the retina and lateral geniculate nucleus proceeds to the primary visual cortex (V1) and then continues rostrally toward the rostral temporal pole.

We see no important difference between untangling to generate a form representation and the additional untangling that leads to an action. The reward system integrates across dimensions to generate abstract decision variables; that is, ones that are correlated with value (e.g., Barron et al., 2017; Blanchard et al., 2015a; Fellows, 2006; Hayden, 2016; Hunt and Hayden, 2017; Raghuraman and Padoa-Schioppa, 2014; Strait et al., 2014; Suzuki et al., 2017). However, unlike the visual system, which has only one major input locus—the eyes—the reward system has many inputs. These inputs must converge on a single target—the motor system. As such, the economic choice system has a serial but dendriform, or fan-in, structure. Some approaches to modeling choice have the convergence occur relatively early so that the brain can create a single common currency representation of value (e.g., Padoa-Schioppa, 2011). However, others have proposed that the valuation system consists of multiple, parallel value computations that do not converge (Passingham and Wise, 2012; Rushworth et al., 2012). From this perspective, input branches may have their own valuation and even comparison processes. These processes may even compete for control of behavior with other ones. The motor system, of course, is not limited to a single effector—the brain has many outputs. The dendriform structure thus likely does not converge on a single point, but instead, it has an early fan-in structure and a smaller later fan-out structure.

For example, when choosing between a salty peanut and a juicy apple, we may initially start by assessing our own satiety (e.g., Livneh et al., 2017). Then the information processed in specialized regions such as insular cortex may combine with form vision information (“red apple and brown peanuts”). We then should also consult our long-term memories (did we get sick the last time we ate peanuts?) and short-term memories that define the context (the price of the snacks, for example). Until the final acceptance of a particular option, the action cost to obtain each option competes (“reaching to the red apple is more difficult than reaching to the brown peanuts”).

The process of integration across domains is similar to combining memory and perception when performing a delayed match-to-sample task. In either case, the ultimate decision is a motor decision—which action to perform. Thus, the ultimate goal of the reward system is to take highly non-linear inputs

and convert it into a format that can be readily sorted into possible actions.

Keeping Irrelevant Information Around

Further evidence for the untangling view in vision comes from considering the fate of category-orthogonal features. In a recent study, Hong and colleagues examined population activity in V1, V4, and IT while macaques passively viewed natural images (Hong et al., 2016). They were interested in the encoding of “primitive” attributes of images, such as position and pose. They called these category-orthogonal features, meaning that the features were not relevant to object categorization—the presumed function of IT. These features are explicitly encoded in early visual areas like V1 (Movshon et al., 1978). Each successive visual area combines its inputs to generate a more abstract form and simultaneously throws away irrelevant factors (DiCarlo et al., 2012; Goodale and Milner, 1992; Lennie, 1998). As a consequence, higher-level form vision areas would presumably have no category-orthogonal features, especially not spatial “where” information, which should be shunted to the parietal stream. Indeed, some have argued that eliminating such information is a necessary precondition for accomplishing the invariant representations associated with later regions in the visual hierarchy (e.g., Edelman and Intrator, 2003; Serre et al., 2007).

Surprisingly, Hong and colleagues find that such features are maintained along the processing hierarchy (Hong et al., 2016) (Figure 4). That is, these features are readily decodable in responses of neurons in both mid- and high-level visual areas. Moreover, category-orthogonal features grew stronger and more decodable when moving from V4 to IT, even as form representations became more abstract. The results confirm earlier hints that such information may be available there (e.g., Baldassi et al., 2013; Hung et al., 2005; Li et al., 2009; Sayres and Grill-Spector, 2008).

Why would this information be preserved? Hong and the colleagues speculate that since this information is available to conscious report, it must be available at the output end. It must, therefore, be carried along the form vision pathway. Doing so helps to avoid binding problems. Supporting this view, tuning in IT—but not in earlier regions—matches human perceptual abilities (Hong et al., 2016). Importantly, preservation of category-invariant features does not require special wiring—it is observed in a standard hierarchical convolutional network modeled after the ventral stream (Yamins et al., 2014). These observations align with the idea that representing object identity is not the end goal of form vision; action is (Krakauer et al., 2017; Pearson et al., 2014; Pezzulo and Cisek, 2016).

The preservation of category-orthogonal attributes, then, is a signature of the kind of untangling processing architecture that implements gradual transformations. Does the reward system carry “choice-orthogonal” attributes? We think so. Perhaps the most well-studied choice-orthogonal feature in economic choice is the spatial position of offers (which, conveniently, is also identified as category-orthogonal by Hong et al.). The evidence for position encoding in reward neurons is somewhat equivocal. Several studies report no spatial encoding (e.g., Gratatan and Glimcher, 2014; Kennerley and Wallis, 2009; Padoa-Schioppa and Cai, 2011).

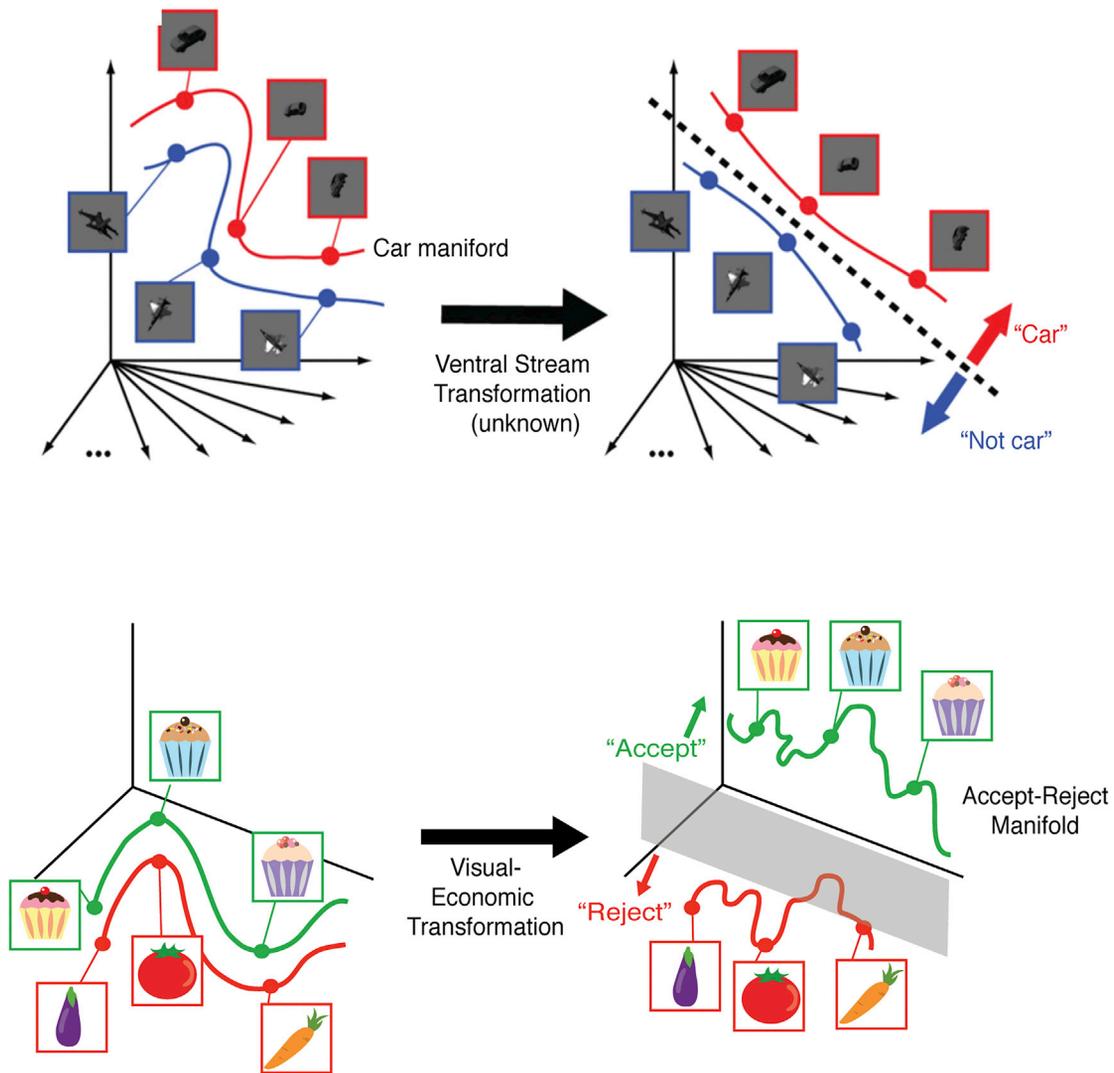


Figure 3. Conceptual Description of Untangling the Input in the Neural Population Vector Space

Visual input in early visual areas still contains object identity manifold but it is highly non-linear. Consequently, a hyperplane cannot cleanly cut it into accepted and rejected options. As with the visual system, information in the reward system becomes untangled as it moves toward the motor system. Figure is based on DiCarlo et al. (2012).

However, some recent studies, using more sensitive tasks or analysis methods, support the idea that there is selectivity for spatial position throughout core reward regions (Roesch et al., 2006; Strait et al., 2016; Tsujimoto et al., 2009; Yoo et al., 2018). This evidence was previously somewhat limited because of the possible confounds with attention or object identity (Padoa-Schioppa and Cai, 2011). We recently performed a study of two core reward regions, orbitofrontal cortex (OFC) and ventral striatum (VS), that was designed to circumvent these problems (Yoo et al., 2018). Specifically, we used the asynchronous presentation of three choice options to control for attention and object identity in a variant of the Wisconsin Card Sorting Task (Sleezer and Hayden, 2016; Sleezer et al., 2016, 2017). These design elements meant that value was determined by the interaction of the option and the attended rule, which varied

randomly on each trial and never had to do with spatial position. By using three options, we could restrict our analysis to incorrect options—meaning we could ignore confounds associated with motor planning and reward expectation. Even with these stringent controls, we found clear selectivity for the positions of offers in all three regions, indicating that at least this one choice-orthogonal variable is observed in two core reward regions (Figure 5). The choice-orthogonal information that has been observed in ostensible reward areas is not proof of the untangling argument. However, it is a feature predicted by the untangling view that is not predicted by modular approaches.

The Reward System and the Motor System

The idea of economic choice as part of a larger untangling process suggests the idea that the sensory system and the motor system

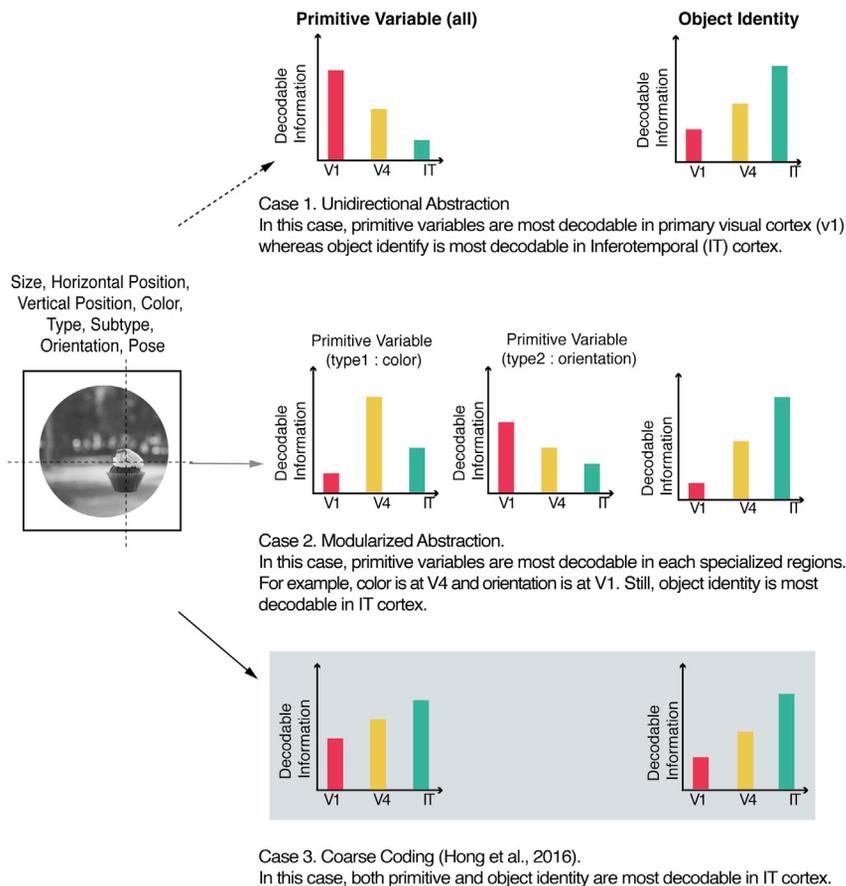


Figure 4. Description of Possible Information Propagation Method when Viewing Cupcake with Specific Size, Position, or Orientation

First hypothesis, the abstraction occurs unidirectionally and primitive variables are dropped. Thus, primitive variables are most decodable in primary visual cortex (V1). Second hypothesis, modularized abstraction makes primitive variable most decodable in different brain regions. For example, color is most decodable in V4 and orientation in V1. Finally, there is case that coarse coding governs information propagation. In that case, primitive variables are strengthened on ventral stream. In all cases, object identity is most linearly decodable in inferotemporal (IT) cortex. Gray box was the result summarizing Hong et al. (2016).

dACC is strongly established (Morecraft and Van Hoesen, 1998; Paus, 2001). Likewise, the OFC is generally classified as earlier in the system, but has ostensible motor signals, albeit ones that are weaker than those observed in dACC (Roesch et al., 2006; Strait et al., 2016; Yoo et al., 2018). The gradual strengthening of motor signals presumably reflects two factors: the inclusion of new sources of motor-related information and the untangling of latent motor information present earlier.

Just as motor information can be found in the reward system, reward information can also be found in the motor system (Cisek and Kalaska, 2010). Consideration

are the start and end of a single larger transformation process. More speculatively, it raises the possibility that motor processing is not categorically different from reward processing, but rather that near the end, motor signals are more untangled, and thus more strongly observed by conventional analysis techniques.

This continuum idea contrasts with a conventional modular view of motor control in which reward and action are naturally cleaved conceptually, anatomically, and functionally (Chen and Stuphorn, 2015; Hare et al., 2011; Padoa-Schioppa, 2011; Rustichini and Padoa-Schioppa, 2015; Wunderlich et al., 2009). Moreover, this continuum view is consistent with ideas, derived from comparative anatomy, that the ventral prefrontal cortex (including vmPFC, ventrolateral prefrontal cortex, vlPFC, and the orbital surface) constitute the rostral end of one of two continuous cortical sheets that begin in the occipital lobe (Finlay and Uchiyama, 2015; Swanson, 2000). Thus, a larger pathway spanning the ventral visual stream and reward system may be reflected in ontogeny.

Supporting this idea, there does not seem to be any categorical shift from reward-related encoding in some regions to motor-related encoding in others. As noted above, motor signals are evident in many ostensible reward regions. For example, the dorsal anterior cingulate cortex (dACC) is a major node of the brain's reward system, one that is identified as the core site of choice in some models (Ebitz and Hayden, 2016; Hare et al., 2011; Wunderlich et al., 2009). The motor function of

of options activates neurons in the premotor cortex and does so in accordance with their values (and, equivalently, with the likelihood of choice, Cisek, 2012; Cisek and Pastor-Bernier, 2014; Glaser et al., 2018). When two options are considered, both action plans are activated simultaneously. They are presumably competing (Cisek, 2006). Note, however, that there are also alternative views (Haith et al., 2015; Wong and Haith, 2017). This simultaneous activation of action plans is also observed in other regions associated with motor planning, such as parietal cortex and superior colliculus (McPeck and Keller, 2002; Scherberger and Andersen, 2007).

As the decision maker deliberates and begins to favor of one the options, the representation of that action grows stronger until a decision threshold is reached (Cisek, 2006; Cisek and Kalaska, 2005; Thura and Cisek, 2014). These observations suggest that these regions are not simply waiting around for the results of the comparison to occur, but that the preparation and comparison take place—in part—within motor regions (Cisek, 2012; Cisek and Pastor-Bernier, 2014; Hunt and Hayden, 2017; Kaufman et al., 2014; see also Peixoto et al., 2018).

The idea of a serial or dendriform organization of the reward system that we present here is consistent with the neuroanatomy. However, it is somewhat oversimplified. First, there are enough interconnections and crossed wires that it may be impossible to place each region at a specific hierarchical level. It may be that the most we can do is to place regions in a rough

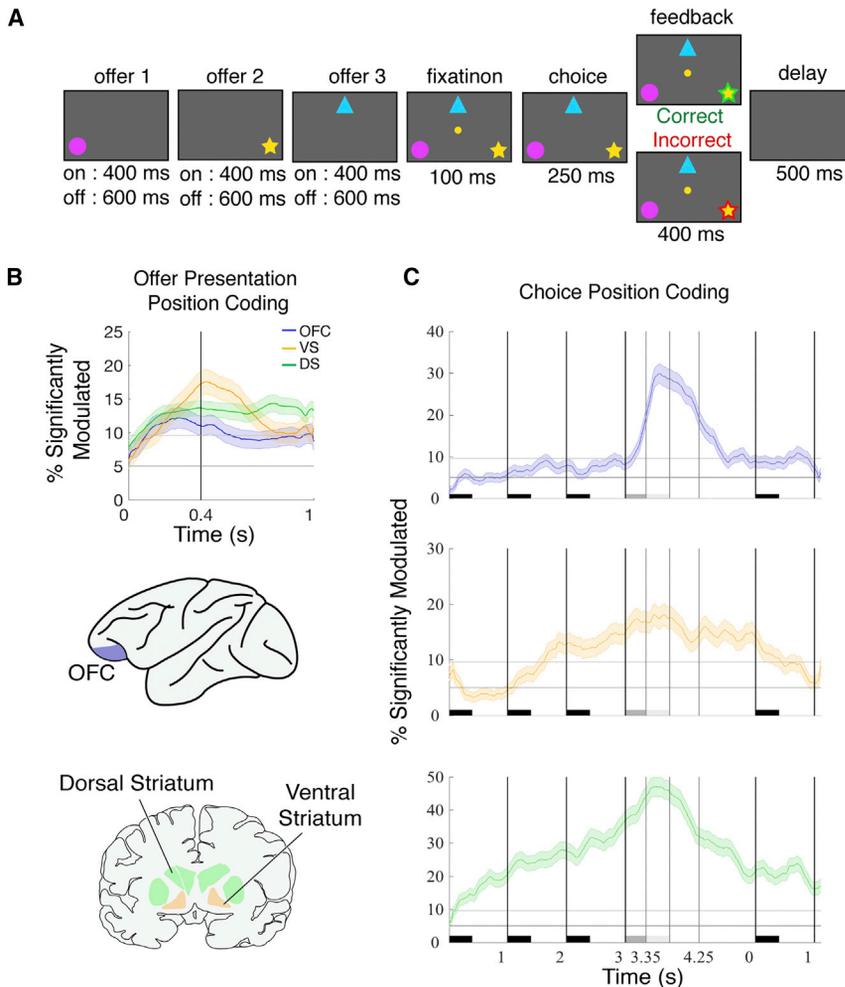


Figure 5. Choice-Orthogonal Information in Early Reward Region of the Brain

(A) Subjects performed a 3AFC set shifting task, where reward was contingent on the rule (color or shape of object) not the position of the object. The rule changed every 15 correct trials, and consecutive rule was randomly selected. Three offers were initially shown asynchronously (offer period) and shown simultaneously in choice period.

(B) Position of the offer is encoded in three core reward regions at offer period (OFC, blue; VS, orange; DS, green). Analysis is done only for the offers with same identity (incorrect/non-rewarding).

(C) Position of the upcoming choice is encoded in the same regions throughout the trial. Although any positional information is orthogonal to choice in current task, core reward regions encode this choice-orthogonal information. Figure modified from Yoo et al. (2018).

The idea that reward and motor processing are parts of a larger continuum relates to an important debate in neuroeconomics: whether choices are made in a goods space or in an action space (Chen and Stuphorn, 2015; Rustichini and Padoa-Schioppa, 2015; Wunderlich et al., 2009; Figure 6). The untangling idea rejects such a functional dichotomy and suggests that choice is made through a distributed consensus process occurring simultaneously in multiple regions (Cisek, 2012; Cisek and Kalaska, 2010; Hunt and Hayden, 2017).

Recently, Cisek and colleagues proposed that biased competition can serve as a useful explanatory framework for

hierarchical position. Second, it appears that regions are not internally homogeneous; there is evidence for structure within areas that complicates the already complex picture (e.g., Freiwald and Tsao, 2010). Third, there are clear feedback effects that have important computational roles (Cumming and Nienborg, 2016; Lee and Mumford, 2003). Finally, by focusing on the cerebral cortex, we ignore the important roles of subcortical structures, including the striatum, the colliculi, and the midbrain, all of which play important economic roles. These critiques apply just as well to the visual system as to the reward system (Felleman and Van Essen, 1991).

Subcortical structures, especially the striatum, the ventral tegmentum, the amygdala, and the basal forebrain, have important contributions in economic decision making. One important question is to what extent these structures have categorically different functions from the cortex. There is at least some evidence that striatum has functional overlap with cortical areas in choice and executive control (Strait et al., 2015; Sleezer et al., 2016, 2017). Likewise, reward prediction error (RPE) is frequently referred to as a critical function of midbrain dopamine neurons, but it can also be observed in cortical areas like dACC (Seo and Lee, 2007).

economic choice (Cisek and Kalaska, 2010; Pastor-Bernier and Cisek, 2011; Pezzulo and Cisek, 2016). In classic work on the ventral visual stream, Desimone and colleagues proposed that different objects are processed in parallel and compete for control of responses (Desimone, 1998; Desimone and Duncan, 1995). In their view, top-down attention refers to the process by which internally generated priorities enhance certain representations. These enhancements take place at multiple levels simultaneously and propagate forward, resulting in awareness of the attended option. Cisek and colleagues provide evidence that these principles apply to the choice system as well (Cisek, 2012; Cisek and Pastor-Bernier, 2014). This idea provides additional motivation for the idea that reward processing is analogous to—and may be an extension of—ventral stream processing.

Non-modular Processing: The Baseball Analogy

Brains are divided into clearly defined regions but their borders are often based on judgments about which aspects of cytoarchitecture are important and how to handle gradual or patchy transitions. Anatomists often disagree on where to place boundaries. Function derives from connectivity, not cytoarchitecture, and

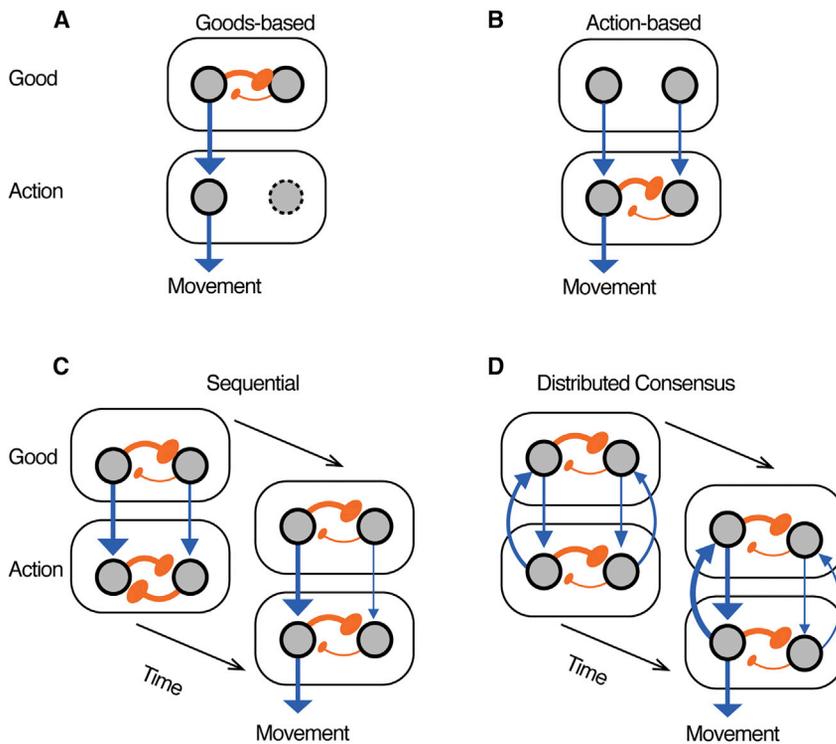


Figure 6. A Few Possible Architectures of Decision Making

(A) In good-based model, decision is made based on competition between represented values. Once winner of the value competition is decided, movement is generated to acquire the preferred option.

(B) In action-based model, values representations never compete between each other. Instead, both representations are sent downstream and those influence a competition between possible action representation.

(C) Sequential architecture proposed by [Chen and Stuphorn \(2015\)](#). In this architecture, the competition occurs in both goods and action space. However, without reciprocal connection, the influence is unidirectional from goods to action space.

(D) Distributed consensus architecture proposed by [Cisek \(2012\)](#). The distributed consensus model assumes reciprocal interactions between the value and the action representation. Competition between action representations will influence value competition via reciprocal connection. The selection of the chosen good and action proceeds therefore in parallel. Figure modified from [Chen and Stuphorn \(2015\)](#).

these two aspects seldom coincide perfectly. But much of the connectivity is not known. In many cases, connectivity is organized along large trans-areal gradients or is patchy (e.g., [Averbeck et al., 2014](#); [Heilbronner and Haber, 2014](#)). These facts pose a challenge to area/function mapping. Nonetheless, we must still account for the demonstrated existence of discrete regions. We propose that a helpful way to integrate these contrasting views starts with an analogy to baseball ([Figure 7](#)).

Fielding a baseball consists of three distinct steps: (1) observing the ball mid-air and catching it, (2) using knowledge about the general state of play to choose whether and where to throw the ball, and (3) throwing it there accurately. This division of functions does not map onto the players on the team. Teams could theoretically assign a single player to watch the ball, a second one to chase down and catch all balls, and a third one to tell the second where to throw it. But it is more efficient to give all fielders autonomy and let them communicate. This has costs—all players must become experts in all outfield functions—but the benefits outweigh the costs.

Consequently, the outfield does not have a functionally modular organization. It has an agent-based organization. The purpose of having multiple fielders is not to add qualitatively new functions. It is to more efficiently cover the large outfield. In a game with very fast-moving play, this is invaluable. Fielders perform modestly different functions, but these functions are not intrinsic; they are determined almost entirely by position.

Consider the difference between a second baseman and a shortstop. One could analyze game footage or examine situations where injured players leave the field during play to identify the essential difference between these two positions. If we

believed that their functions were catching, deciding, and throwing, we could point to data showing that, perhaps, the shortstop catches the ball more often than the second baseman, and the second baseman tags the runner more often. The conclusions we draw would be accurate, but would miss the much larger point: both players observe, catch, decide, and throw. Measuring their differences does tell us something about the small differences in skills needed for these two positions. But the major difference is just their location on the diamond.

Imagine removing a player to understand his or her function. A “lesion” to the center fielder, for example, will result in a rapid reorganization (because all fielders are experienced enough to adapt effectively to new situations). Left and right fielders will move toward the center, second base and shortstop will move a bit backward, and so on. This rearrangement will result in two inefficiencies. First, the average distance between a player and a hit ball will be greater, so reaction times will be slower and catching likelihood will be lower. Second, players will be less familiar with their new positions and will not play as effectively (like a brain recovering from a stroke, this problem will fade as players adjust to their new roles). There will not be a complete loss of any specific fielding function. Of course, modularity exists on a continuum. Some positions, like the first baseman, are highly specialized and are more difficult to cover even with flexible players. An absent pitcher will result in complete inability to play baseball. But much of the field is moveable.

Our metaphor is limited when applied to the brain; in particular, baseball is a highly agent-based system. However, much of the brain is serial and hierarchical in structure ([Badre and Nee, 2018](#); [Hunt and Hayden, 2017](#); [Koechlin et al., 2003](#); [Rushworth et al., 2011](#); [Siegel et al., 2015](#)). Sensory areas are early and motor areas are late, and latencies and neuroanatomy can hint at the hierarchical positions of many regions ([Felleman and Van Essen,](#)

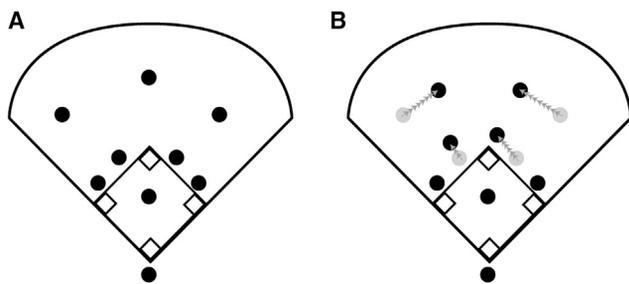


Figure 7. Baseball Fielding Positions

(A) The regular fielding position with nine players. (B) If we could “lesion” a center fielder, the other players would adjust positions slightly to cover the field efficiently. The flexible roles of each player allow for flexibly responding to unexpected changes in play and lead lesions to have minimal effects.

1991). Nonetheless, the baseball metaphor provides a starting point for thinking about a distributed choice system.

Serial and Repeated Micro-computations that Can Produce Choice

What are simple computations that, when repeated and organized serially, will produce accurate choices? If we think of the process of choice as an untangling from an input space to an orthogonal output space, then any step that performs a single step of untangling would serve this purpose. For an accept-reject decision, one candidate would be any process that up-weights (even if only weakly) the representation of options that ought to be accepted and down-weights options that ought to be rejected. For a multi-option choice, that would be any process that compares options and adds even a small amount of weight to the option that is likely to be favored.

But is there a single computation that can flexibly handle both accept-reject and multi-option choices? We suspect that there is, but first, they need to be unified theoretically. Some foraging-inspired models emphasize the idea that multi-option choice is, in practice, a specialized form of single-option (accept-reject) choice (Blanchard et al., 2015a; Hayden, 2018; Kacelnik et al., 2011; Pearson et al., 2010; Stephens and Krebs, 1986). Kacelnik and colleagues propose that options are evaluated largely independently of each other in a horse-race type comparison (Kacelnik et al., 2011). That is, the evaluation process for each option varies in duration; faster evaluation occurs for more valuable options. The option that is accepted fastest is the one that is chosen. The comparison then occurs indirectly. Likewise, a different set of models, attention-limited choice models, propose that options are evaluated independently and asynchronously, but the first option to pass a threshold still wins (Hayden and Moreno-Bote, 2018; Krajbich and Rangel, 2011; Rich and Wallis, 2016). Although neither model is definitively favored at this point, they both suggest ways in which multi-option choices can be reduced to single-option ones.

Evaluation and thresholding do not need to be distinct. If the evaluation at each point is relative, then no additional thresholding operation is required (other than the one that leads to the commitment to perform the action). This means that each stage would need some information about the choice threshold. Note

that this calculation is non-trivial. It involves estimating the value of the background (that is, the value expected from rejecting the current offer and taking the next best one), which is often uncertain in size and timing (see also the closely related ideas of biased competition for economic choice discussed above; Thura and Cisek, 2014).

We believe that divisive normalization, or something much like it, might be the top candidate for this process (Louie et al., 2015; Yamada et al., 2018). Divisive normalization, which is another concept imported from visual neuroscience, suggests that overall activation in the pool of neurons reversely controls the activity of the individual neural activity (Heeger, 1992). Divisive normalization has been successful in explaining neural activity in various systems beyond vision (e.g., olfactory, Olsen et al., 2010) and would be a canonical computation in the brain (Carandini and Heeger, 2011). In the context of value, it would be a scaling of value encoding relative to the other options available. In the economic context, divisive normalization is normally thought of as a mechanism for implementing range invariance (Louie et al., 2015). However, this underestimates its usefulness. Divisive normalization (or other normalization processes, for that matter) may be sufficient to compute the key decision variable for economic choice—the relative value of pursuing the attended option (Strait et al., 2014). A normalized value, subject to a threshold, is sufficient to determine the choice.

There is a good deal of evidence that evaluation in the brain is done in a relative manner. For example, much evidence supports adaptive coding (Padoa-Schioppa, 2009), mutual inhibition (Hunt et al., 2012; Jocham et al., 2012; Strait et al., 2014, 2015), and divisive normalization (Louie et al., 2015; Yamada et al., 2018). In all cases, value-related activity depends on the options available. Likewise, mutual inhibition has been observed in several reward regions and suggests some mechanism of value comparison (Hunt et al., 2012, 2014; Strait et al., 2014). Our purpose here is not to adjudicate between approaches but to show that multiple converging lines of evidence point to the same basic idea. To wit, simple operations allow for incremental relative valuation that, when aggregated, can produce choices. We propose that relative valuation, whatever its specific form, is something that occurs throughout the hierarchy that transforms inputs to outputs. Each stage at which it occurs participates in the gradual transformation. The result of this gradual untangling process will be that individual regions cannot be classified as pre- or post-decisional (Azab and Hayden, 2017; Figure 8). Rather the decision will occur across multiple regions in a series of steps, like a relay race.

The concept of iterated simple computations has parallels in the ventral visual system. According to some theories, feedforward functional units perform a common computation: take the afferent input, apply a nonlinearity, adjust the synaptic weights that are being linearly summed, and normalize by the aggregate activity of a nearby neural pool (DiCarlo et al., 2012; Riesenhuber and Poggio, 1999). Repetitive computation throughout multiple layers is also the essence of deep convolutional neural networks, which have recently proven useful in visual neuroscience (Kriegeskorte, 2015; Krizhevsky et al., 2012; Yamins et al., 2014). The architecture consists of repetitive local operations like nonlinear thresholding, normalization, max-pooling, and convolution until a final decision is made. These results provide further

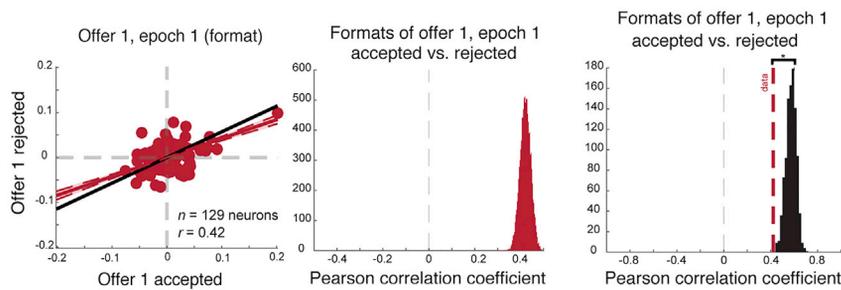


Figure 8. Lack of Pre- and Post-decisional Signal in Reward Regions of the Brain

The subject performed two sequential asynchronous tasks that varied reward amount and probability. Initially, the neural response was regressed against values of accepted and rejected first offers. Then the correlation between the regression coefficients was investigated. If there is any positive correlation, it indicates that these neurons signal the value independent of whether the option will later be chosen to some degree. Figure is from [Azab and Hayden \(2017\)](#).

support for the idea that neurally inspired simple computations, repeated in sequence, can perform gradual nonlinear untangling.

Implications of the Choice Microarchitecture

One implication of this repeated micro-computation idea is that evaluation, comparison, and thresholding operations can be implemented within a single computation ([Cisek and Pastor-Bernier, 2014](#); [Hunt and Hayden, 2017](#)). Evidence for this hypothesis comes from the strong multiplexing and even mixed selectivity observed in many reward regions ([Enel et al., 2016](#); [Rigotti et al., 2013](#); [Fusi et al., 2016](#)). The reason is that mixed selectivity allows linear readout more readily ([Fusi et al., 2016](#); [Rigotti et al., 2013](#)). That is, the non-linearity observed in representations directly contributes to linearity in the readout.

Another implication of the untangling idea is that information about value is stored in a distributed manner, across the entire processing hierarchy. Thus, not only are the computations associated with comparison distributed, but the storage of learned information is distributed as well. And, importantly, it is located in the same regions that perform the comparison. This is not to say that the distribution is necessarily equal—regions can have specialized forms of information. But no value information is localized to specialized value-storage regions.

Linking learning to choice may offer insight into another puzzle. The neural structures that support the representation of offers are generally reactivated when rewards are received ([Blanchard et al., 2015b](#); [Farovik et al., 2015](#); [Howard et al., 2015](#); [Kahnt et al., 2010](#); [Tsujiimoto et al., 2009](#); [Wang and Hayden, 2017](#)). There is no obvious reason why the brain must be organized this way; indeed, in a modular system, there is no reason why monitoring and comparison would not be implemented by different, specialized regions. However, if the comparison occurs through serially organized reweightings of inputs, and those weightings serve to store values, then they need to be trained somehow. That training would most naturally occur directly, at the time of reward receipt. Thus, the responses to received reward could be a reflection of the learning processes that serve to create value representations.

Standard views hold that the brain explicitly computes and stores neural representations of value ([Levy and Glimcher, 2012](#); [Montague and Berns, 2002](#); [Rustichini and Padoa-Schioppa, 2015](#)). If the choice is reconceptualized as an untangling of inputs into actions, then there is no specific stage in the middle that can be called a value stage. At a micro-level, there is no value representation per se; just a partially reweighted version of the information at the higher level ([Balasubramani](#)

[et al., 2018](#)). At a macro-level, early stages don't have access to the information available at later ones, and later stages have already gone relatively far down the road of creating motor plans (i.e., untangling their inputs). This does not mean that that value is not represented in the brain—the reweightings themselves are an implicit representation value. But in this view, the value is not represented explicitly: it is an emergent property ([Hunt and Hayden, 2017](#)).

Testable Predictions for the Untangling Hypothesis

The idea of untangling is an extrapolation of recent trends in both form vision and economic choice literature. The evidence in favor of this view is suggestive but not dispositive. The following predictions, if validated, would lend support to support our view.

First, we predict that future anatomical research will provide firmer evidence that the economic choice regions have a hierarchical organization with a fan-in structure. This view is currently supported by at least some functional measures (e.g., [Hunt et al., 2012](#)). However, our understanding of the connectivity and hierarchical structure of the reward system is impoverished. The careful work laying out the organization of the visual system was critical for establishing the processing structure there ([Maunsell and Van Essen, 1983](#); [Felleman and Van Essen, 1991](#)). If a similar organization is found in the reward system, it would support our ideas.

Second, we predict that future neuroanatomy will demonstrate evidence of gradients of function that span multiple anatomical areas. That is, the sharp borders found in textbooks will be supplemented with evidence for overlaid larger patterns showing cross-areal similarities and smooth changes.

Third, we predict in direct comparisons of responses in brain regions within the choice pathway, that choice-relevant information will be available throughout, but both stronger and more linearly readable in later stages. We anticipate intermediate representations for economic decision making in middle stages. Current research on the economic choice system, especially physiology, tends to focus on a small number of areas (e.g., ACC, dlPFC, OFC). We predict that as scholars begin to use the same tasks in new regions, they will turn up more quantitative, not qualitative, differences in function.

Fourth, mixed selectivity enhances linear decodability by allowing the creation of high-dimensional representations ([Rigotti et al., 2013](#); [Fusi et al., 2016](#)). Thus, we predict that the degree of mixed selectivity—and the dimensionality of representations—will be increased at the later stages of economic decision making.

Fifth, we predict that future combined lesion functional measure studies will show that those intact regions will partially take over the economic functions of hierarchically adjacent regions that have been experimentally lesioned. If these functions turn out to be part of a continuum (see the third prediction, above), then the takeover of the function will also be quantitative.

Sixth, untangling often combines information (Pagan et al., 2013). In Pagan et al., this was the identity of the memorandum and probe. In economic choice, there are two important cases where decision makers must combine information. When evaluating an option in a multifactorial choice, we must combine across dimensions (Blanchard et al., 2015a; Raghuraman and Padoa-Schioppa, 2014). And, when selecting between two options, we must compare them and choose a single preferred one. We predict that hierarchically later areas will show greater integration across dimensions for both processes.

Seventh, we predict that future studies will confirm suggestions that category-orthogonal information is represented late in the processing hierarchy (Hong et al., 2016). Furthermore, we predict that this information will be more linearly readable in later structures (this hypothesis has not been tested). Finally, we anticipate that this information will be functionally causally related to aspects of choice that require it—and not just functionally irrelevant but decodable information.

Conclusion

There are many examples of distributed decision making systems that consist of largely similar elements that, when working together, can produce good choices. The most famous is the swarm decision makers: bees and ants (Couzin, 2009; Sumpter et al., 2008). In honeybee decisions, each participating bee evaluates one option at a time and the swarm collectively chooses whenever a sufficient number of individuals vote for that option. Comparison occurs indirectly (*cf.* Kacelnik et al., 2011). The process is slow—it takes several days and several hundred bees to make a good decision. But it is robust—individual bees don't require any special training, nor is the system vulnerable to loss of particular specialized individuals.

The similarities between swarm decision making and neuronal decision making are striking (Couzin, 2009). However, the most extreme distributed perspective cannot be readily reconciled with the brain's organization. In particular, the bee swarm is a parallel decision making system but the brain appears to have a serial and hierarchical structure. Nonetheless, a serially organized but distributed choosing system does appear consistent with many neuroscientific data.

In model-based decisions, the brain forms a model of the external world (e.g., a model about state changes according to actions) and makes a decision based on that model (Doll et al., 2015). Earlier accounts involved explicit representations as a foundation for model-based decisions. However, recent evidence suggests that architectures with emergent properties (e.g., in a neural network) can generatively model the world and plan and make decisions based on that model (Hassabis et al., 2017). While an elaboration of these ideas is beyond the scope of this Perspective, our view does not exclude model-based decision making.

This view means that there are real—quantitative but not qualitative—differences between regions. Lesions to an early region will result in some deficits and lesions to a later region will result in others. For example, lesions to OFC will cause reward-association deficits, lesions to vmPFC will cause value-comparison deficits, and lesion to dACC may cause deficits when actions are involved (Kennerley et al., 2006; Noonan et al., 2010; Rudebeck et al., 2006). These lesions may produce qualitative differences—and may even produce double dissociations—even if the underlying organization is a functional continuum (Plaut, 1995). This does not prove that the mind is not modular, even if it demonstrates the difficulty of inferring modularity from lesions.

Ultimately, we are proposing that while many brain functions are modular, the economic choice is not. We suspect that economic choice may be different from other brain functions that have more circumscribed roles in behavior. Economic choice is defined in terms of behavior—and value is defined by revealed preference. If a monkey chooses differently on some subset of trials, that proves only that my value was different on those trials, not that some other process intervened and made me choose against my value function (Sugrue et al., 2005). In other words, economic choice, as traditionally defined, refers to the selection of actions based on any factor that influences value.

Consequently, it is difficult, even theoretically, to separate value and economic choice from any factors that influence choice. For example, information stored in memory, to the extent that it can influence choice, is a value-related memory. And visceral information, to the extent that it influences choice, has an economic role, and so on. The fact that value can only be identified from behavior and cannot stably differ from behavior, suggests that economic choice must encompass all factors that drive behavior. This definition of economic behavior has been called circular, but we think it is not—it's just that, when carefully considered, the economic choice cannot be differentiated from the entirety of behavior. This observation is only problematic if we wish to delimit what is and is not an economic region of the brain. But if we are willing to imagine that economic choice is so broad that it takes up almost all of cognition, we cannot be surprised that it takes almost all of the brain.

Our view seems, by design, to seek to go as far as possible without invoking explicit representations. We are aware that there are good reasons to expect that the brain would use explicit representations in some cases (e.g., Griffiths et al., 2010; Lake et al., 2017). Nonetheless, there is a good deal of room available to explain economic choice before positing overt representations. Consider attention. It is very possible that there is no explicit representation of attention anywhere in the brain. Instead, attention is usefully thought of as a name for a process that modulates visual representations. We argue that value is, similarly, a convenient name for any process that modulates action plans or choices. It has obvious effects on the representations of other variables in other brain systems and biases behavior, but it is not computed as the end product of specific, dedicated system.

In the final judgment, this view may appear trivially true. That is, one could, in theory, reconceptualize all of the cognition as a driver for choice, but would such an exercise be intellectually

sterile? Our argument is that doing so has at least one important benefit: it explains why economic choice is so widely distributed while almost all other cognitive functions (audition, face perception, balance, etc.) can be localized.

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