can be exposed following the colonization of a new environment in which different induced phenotypes are beneficial, thereby exposing this variation to selection and facilitating adaptive evolution [5–7]. In this study, however, the derived selected variants identified in *PREP* and *PRKAR1A* were not found in any nearby lizard populations, and simulations support the hypothesis that these alleles arose recently within the Pisgah population. This instead suggests that adaptation to the dark substrate of the Pisgah Lava Flow occurred through selection on novel mutations that arose in the Pisgah population after it colonized the lava flow, rather than through selection on standing variation present before colonization. Thus, in this example plasticity allowed sufficiently long survival of the Lava Flow population for novel beneficial mutations to appear, which were subsequently subject to natural selection. The findings of Corl and colleagues [11] provide an extended and empirically derived view of the role of plasticity in facilitating adaptive evolution beyond the expectations of the 'plasticity-first' hypothesis, such that plasticity can permit the evolution of novel genotypes and phenotypes and facilitate eventual adaptation to new environments, even in the absence of relevant standing variation at the time of colonization.

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Neuroscience: Intracranial Recordings of Value

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The role of orbitofrontal cortex in value-based choice is well-established from animal research, but there are challenges in relating neurophysiological recordings from animals to equivalent data from humans: a new study bridges this gap.

In daily life we are constantly making decisions: what to wear, what to have for lunch, where to go on holiday in summer. In order to make choices between multiple alternatives, the brain somehow needs to compare them using a 'common currency'. One hypothesis is that the brain facilitates this by computing a single value for each alternative by considering multiple sources of evidence indicating how good the option is. For example, if you wanted to decide whether or not to watch a particular movie tonight, you may consider how good the trailer is, whether your friends liked it or not, whether it has good reviews, and your previous experiences with movies of the same genre. All these factors are summarized in a single value, enabling us to easily compare completely

different options, like comparing 'Love Actually' to 'Die Hard'. In this issue of *Current Biology*, Saez *et al.* [1] describe a rare and interesting dataset obtained from intracranial recordings in humans that characterizes such a value signal in orbitofrontal cortex (OFC).

Saez *et al.* [1] collected multi-electrode electrocorticography recordings from OFC in epilepsy patients performing a choice task. These patients had electrode grids and/or strips implanted in order to find the epileptogenic focus before surgery. Electrodes located away from epileptiform activity provide a rare opportunity to record neurophysiological data directly from human OFC in awake volunteers. During the task, the patients were repeatedly asked to choose between a fixed amount of money and a gamble. For example, on a given trial the patient might be asked to choose between a $10 fixed reward and a 50% chance to get $30. These choice values were randomly varied across trials, such that on some trials the patients would tend to choose the fixed reward, and on other trials they would tend to gamble. Several types of decision variable were encoded in response to the task in high-frequency activity (70–200 Hz oscillations) in OFC. Specifically, fast signals encoding the value of the alternatives, as well as risk (variance of the outcomes) and regret ('counterfactual' feedback on an unchosen option), were identified. These signals were found in response to both choice and outcome presentation. OFC activity also contained sustained activity in response to the previous trial of the task.

OFC has long been implicated in animal research of value-based choice using neurophysiological recordings made principally from one of its subregions, area 13m [2–4]. There are challenges, however, in relating these recordings to equivalent studies of value processing in humans, which are most often conducted using functional magnetic resonance imaging (fMRI). This is in part because the two types of data are of very different form. fMRI only measures blood flow changes arising as a consequence of neural activity, and so has a sluggish temporal resolution. Additionally, due to the location of OFC within the brain, its signal suffers from artifacts caused by differences in magnetic susceptibility at interfaces between air and tissue [5]. It is certainly the case that robust and reliable correlates of value can be found in this region using human fMRI [6,7]. However, value signaling in humans is more often found in ventromedial prefrontal cortex, an area medial to area 13m and with distinct connections to other brain regions [8,9] (Figure 1).

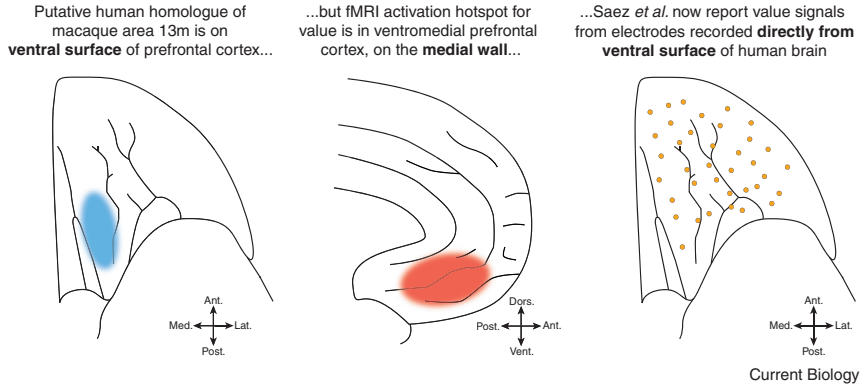

Figure 1. Correlates of value for decision making in ventral and medial prefrontal cortex.
Numerous electrophysiological recording studies in non-human primates have found correlates of value during decision making tasks in orbitofrontal cortex, located on the ventral surface of the brain. However, these recordings have primarily focussed on area 13m, whose putative human homologue is shown in the left panel [9]. By contrast, value correlates in human functional magnetic resonance imaging (fMRI) studies have tended to cluster in ventromedial prefrontal cortex, as shown in the middle panel [6–7]. Saez *et al.* [1] now report value signals in electrocorticography data recorded from human epileptic patients from across the ventral surface of prefrontal cortex, including the homologues of area 13m and other areas previously recorded in non-human primates.

The intracranial recordings of Saez *et al.* [1] overcome some of these challenges in relating animal and human data by providing high temporal resolution data from regions directly homologous to area 13m (and other portions of OFC) in humans. The fact that these recordings show value signaling provides support for OFC having comparable functionality in different species. Note that the recordings taken here are still by far not at the micro-level of animal research. In animal research, measurements are typically taken at the single cell level. The recordings presented here are in the order of hundreds of thousands of neurons, and cannot be directly compared to animal single cell recordings, but they are certainly much easier to link to animal data than human neuroimaging data. This unique dataset also helps to explore the relationships between neural activity at the single-cell level, field potentials, and blood-oxygen-level-dependent signals as measured with fMRI.

Electrocorticography recordings also enable separate analyses of broadband and high frequency activity. Measuring high frequency activity with electrocorticography is more straightforward than with other methods used to study temporal dynamics of brain processes in humans (such as electroencephalography). The new paper of Saez *et al.* [1] is one of the first to analyse the dynamics of OFC activity in high frequency bands during human value-guided choice, again providing a strong link to equivalent analyses in animal recordings [10].

Also of note is the finding that OFC not only encodes current value but also shows sustained activity in response to value-relevant factors from the previous trial. Sustained activity in OFC in response to value has previously been seen *across* trials in associative learning tasks [11]. Sustained responses have also been detected in OFC *within* trials when choice alternatives were presented sequentially on each trial [4].

But given that the trials in this study are stand-alone choices and minimal learning is expected to take place throughout the task, sustained activity might not be expected here. Kennerley *et al.* [12] have previously suggested that keeping track of value history is a way to compare value on the current trial to past rewards. Encoding relative value could be a more efficient way of representing value than fixed value representations, because it allows processing in different scenarios in which value may vary greatly [13].

One big difference between the new study [1] and how studies on value-based choice with human participants are usually conducted is that here, understandably, the patients could not be paid for their participation. Their motivations may also differ from the college undergraduate populations typically used in human studies. This seems like a minor detail, but these decision-making tasks are typically incentivized with money. The effect of not incentivizing the task may be the cause of the fact that most subjects in this study were risk-neutral, meaning they did not show a preference for the fixed reward or gamble. Typically, in incentivized tasks participants are shown to be somewhat risk-averse, avoiding the gamble even if it has a higher average pay-off [14], though there is much individual variation. On the other hand, subjects in the present study did reliably choose the option with the higher probability of winning, implying that their choices were motivated despite not receiving direct financial compensation. To what extent it matters whether a choice in an experiment has a 'real' monetary outcome for encoding of value factors is unknown but would be useful to investigate to know whether our decision-making studies are accurately mimicking real life choice scenarios [15].

Different types of decision variable have been related to OFC activity in the literature [4,16,17], which makes it unclear which information OFC actually encodes. The Saez *et al.* [1] paper has resolved some of this conflict by showing that OFC encodes many decision variables at the same time. The results indicate that OFC encodes variables including expected value, reward, reward prediction error, risk and regret. A next step in understanding value-based decision-making in the brain might be to try to understand what underlying mechanism gives rise to these manifold decision variables. For example, one computational account of decision-making proposes that certain decision variables arise as the consequence of different decision speeds across different trials [18].

In short, this rare dataset [1] has enabled us to fill in some of the gaps left by conventional methodology. Firstly, these results enable us to better link animal and human research findings on value representations in the brain. Also, the value information carried by brain activity of different frequencies is illuminated here in a way that could not be achieved in humans otherwise. Besides this, the fact that sustained activity to the previous trial was found in a task where each trial is independent and no learning takes place gives additional evidence to the idea that OFC flexibly adapts its value encoding across trials. Finally, this paper resolves some of the conflict surrounding the question of what type of value information OFC actually encodes by showing it appears to be encoding many value-relevant factors at once. It will be exciting to see how similar intracranial recordings will aid our understanding of neural mechanisms of human decision-making in the future.

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