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Multiple signals in anterior cingulate cortex

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Activity in anterior cingulate cortex (ACC) has been linked both to commitment to a course of action, even when it is associated with costs, and to exploring or searching for alternative courses of action. Here we review evidence that this is due to the presence of multiple signals in ACC reflecting the updating of beliefs and internal models of the environment and encoding aspects of choice value, including the average value of choices afforded by the environment ('search value'). We contrast this evidence with the influential view that ACC activity is better described as reflecting task difficulty. A consideration of cortical neural network properties explains why ACC may carry such signals and also exhibit sensitivity to task difficulty.

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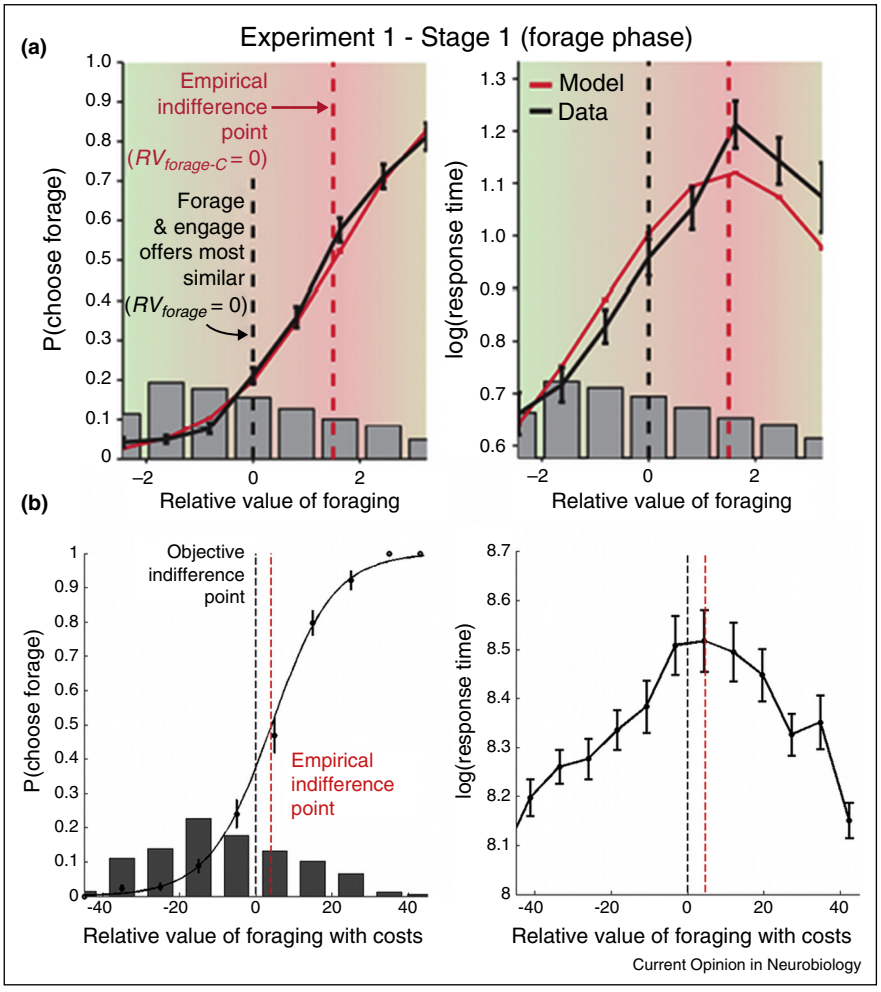
When humans and other animals take a course of action they usually do so because they believe the benefits of doing so will outweigh the costs. There is an evolving understanding of the mechanisms underlying evaluation of one well-defined choice against another that have been linked to ventromedial, orbital prefrontal, and intraparietal sulcal cortex [1,2••,3,4••,5]. There are also, however, times when animals decide whether it is worth acting at all or evaluate whether it is worth continuing to engage in the current behaviour or to explore alternatives. This distinct pattern of decision-making is linked to ACC; ACC manipulations affect the ability of animals to initiate any action at all [6], weigh up the costs and benefits of actions [7,8••], switch between actions as their values change [9,10••], or explore alternative choices [11••]. A series of recent studies have demonstrated the presence of activity changes in ACC that correspond to the types of signals that would be needed to guide such behaviour; these signals encode the values of actions [7,12••,13,14,15,16••,17••,18••], the average value of alternative courses of action in the environment ('search value') as opposed to the current or default course of action [19–21], exploration and evaluation of hypotheses about the best course of action to take [22,23••,24], and reflect updating of decision-makers' beliefs and internal models of their environments [25,26]. Not only are such signals found in ACC but they are weak or absent in regions such as orbitofrontal and ventromedial prefrontal cortex that carry other value signals [12,19,20,22].

In addition, however, ACC has also been linked to 'conflict monitoring' — the process of detecting when two competing choices might be made during a difficult task [27]. Detecting response conflict and task difficulty is important if mistakes are to be averted. Recently it has been argued that ACC activity interpreted as reflecting value signals has been confounded with difficulty and so it has been argued that such ACC activity is more parsimoniously interpreted as simply reflecting task difficulty [28]. Here we review evidence, first, that value signals and, second, model update signals can be separated from any effect difficulty exerts on ACC activity.

For example, a recent study [19] investigated how people decide whether to explore a set of alternative choices or stick with the opportunity to make a 'default' choice. The value of exploring was encoded by a 'search value' signal in ACC indexing the average value of the set of alternative choices that might be taken. In addition to *search value*, ACC activity was also influenced, in a negative fashion, by *engage value* (the value of the default option) and *costs* incurred by searching. This pattern of positive and negative modulations is suggestive of a comparison process taking place within ACC that could inform decisions about whether or not to explore, or 'forage' amongst, the alternatives.

Figure 1a, however, summarizes how difficulty might be confounded with the difference between *search* and *engage value* — a quantity sometimes referred to as the 'relative value of foraging' or RVF [28]. The probability of behavioural change — searching as opposed to 'engaging' with the current default — is plotted on the ordinate as a function of RVF. A confound between RVF and difficulty arises if subjects are biased to take the default. Even if the experiment examines decisions equally on either side of the objective indifference point — the point at which searching and engaging objectively have the same value — it is still possible that the sampling is unequal with

Figure 1



Avoiding confounds between value and difficulty. (a) Foraging frequency (left) and difficulty, as indexed by log(RT) (right), as a function of RVF in an experiment claiming value signals and difficulty have been confounded in ACC [28]. The black line indicates behavioural data and the red one the corresponding model fit. The grey bars are the sample sizes and the dotted lines are the two indifference points (red = subjective or empirical and black = objective indifference point, i.e. where the value of searching and engaging are objectively equal; 'RV_{forage} = 0'). The participants tended not to forage and to be inaccurate. For example, foraging frequency barely reaches 80% even on the right hand side of the left panel and the participants' empirical indifference points were far from the objective indifference point. **(b)** After adequate task training and instruction in a version of the task employing a balanced and evenly sampled range of search and engage values in which decisions are non-trivial and require value comparison [19] several features of the experiment, participant performance, and data are notable: (i) participants balance all the factors that should influence decision-making in an approximately rational manner and the point of empirical indifference is close to the objective indifference point meaning that ii) data are sampled from both left and right of decision space ensuring foraging values and difficulty decorrelation; iii) Log(RT) decreases either side of the empirical indifference point in an approximately similar manner confirming foraging values and log(RT) are not correlated. Foraging decisions plotted (similar format to a) as a function of RVF (based on all three variables that should influence behaviour: search value, engage value, and an additional factor related to the cost of foraging). Adapted from [19,28].

respect to the subjective or empirical indifference point — the point at which a given participant has no preference between the options. The confound arises because decisions close to the subjective indifference point are the most difficult to take [for example, they are associated with long reaction times (RTs)]. If participants are very biased to nearly always take the default option then RVF and difficulty both increase together across much of the decision space.

Experiments addressing this criticism must contain certain obvious features. First, a broad and evenly distributed range of search and engage value must be tested. However, at the same time, it is crucial that decisions are not trivially easy and that some value comparison occurs on each trial. Second, it is imperative that participants make decisions that really are guided by option values and do not always simply engage with the default option. One way of ensuring this is simply to provide adequate task training and