42 Choice Values: The Frontal Cortex and Decision Making

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ABSTRACT Actions are chosen on the basis of expectations about the benefits they will yield. Areas in the brain's frontal lobes are important for making decisions about which choice it is best to take. In functional magnetic resonance imaging experiments, the ventromedial prefrontal cortex exhibits signals related to the values of potential choices, and the activity pattern is consistent with the emergence of a decision. Ventromedial prefrontal cortex lesions disrupt value-guided decision making. Another frontal lobe area, the anterior cingulate cortex, is also important for value-guided decision making. There is some evidence suggesting that anterior cingulate cortex is especially involved in the selection of an action in the light of the rewards that will follow and the effort that will be invested. More fundamentally, it may be concerned with the computation and comparison of values needed for decision making during foraging. During foraging, the key decision is whether to engage and pursue the default choice, or whether the foraging opportunities available elsewhere in the environment mean it is better to switch away from the current behavior and pursue other alternatives.

When we make a movement, we need to make sure that it is executed correctly. We have to ensure that muscles and joints move in such a way that the limb is directed to the desired target location and the hand is configured correctly. Rather than looking at the neural mechanisms that determine *how* an action is executed, this chapter instead focuses on the cortical mechanisms that underlie *why* one action is chosen instead of another. It focuses on the cortical mechanisms (figure 42.1) that underlie selection of a choice on the basis of the value of its consequences.

Value signals in prefrontal cortex for guiding decisions

The ventromedial prefrontal cortex (vmPFC) and adjacent medial orbitofrontal cortex (mOFC) play a central role in choice selection. For some time, it has been clear that activity in the vmPFC/mOFC region is correlated with the values of stimuli and choices (Kable & Glimcher, 2007; Lebreton, Jorge, Michel, Thirion, & Pessiglione, 2009) and it now seems likely that the vmPFC/mOFC is involved in the actual making of the decision itself. When people make a decision between two potential choices, the vmPFC/mOFC exhibits a signal that suggests it is comparing the values of the choices. For example, Boorman, Behrens, Woolrich, and Rushworth (2009) used functional magnetic resonance imaging (fMRI) to measure blood oxygen level–dependent (BOLD) indices of brain activity in human subjects while they made a series of decisions between two different choices associated with different numbers of reward points. The points won by the subjects were translated into a monetary payment at the end of the experiment. The decisions were difficult in the sense that the reward associations contained two elements: a certain number of points (*reward magnitude*), which changed randomly from trial to trial, and a certain probability of the points being delivered (*reward probability*), which slowly changed over the course of a series of decisions. Therefore, in order to choose effectively, subjects had to consider both of the elements that composed each option.

Boorman and colleagues found vmPFC/mOFC encoded the difference in value between the option that was chosen and the option that was rejected in each decision (figure 42.2). They referred to this as a relative chosen value signal. At the time that a choice is made, the vmPFC/mOFC BOLD signal becomes positively correlated with the value of the option that is chosen and negatively correlated with the value of the option that is being rejected (figure 42.2). One interpretation of this pattern is that vmPFC/mOFC activity increasingly reflects the value of the option that is to be chosen, and at the same time it is less and less activated by the value of the option that is to be rejected. When this process is complete, the decision is made.

Several other fMRI studies have confirmed the existence of relative chosen value signals in vmPFC/mOFC (de Martino, Fleming, Garrett, & Dolan, 2013; FitzGerald, Seymour, & Dolan, 2009; Philiastides, Biele, & Heekeren, 2010; Wunderlich, Dayan, & Dolan, 2012).

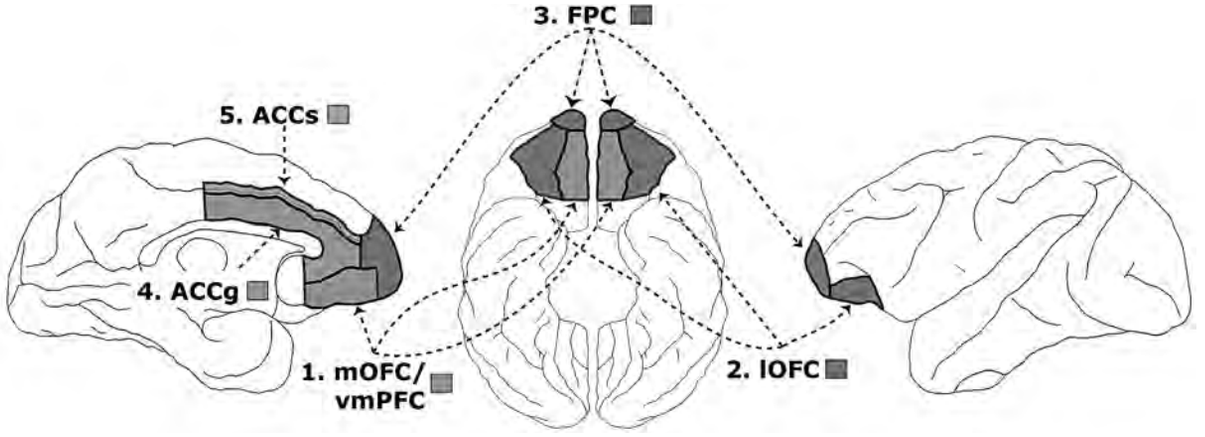

FIGURE 42.1 Frontal brain regions, in the macaque, involved in reward-guided learning and decision making. Abbreviations: vmPFC/mOFC, ventromedial prefrontal cortex/medial orbitofrontal cortex; lOFC, lateral orbitofrontal cortex; ACCs, anterior cingulate cortex sulcus; ACCg, anterior cingulate cortex gyrus. (Adapted from Rushworth et al., 2011.)

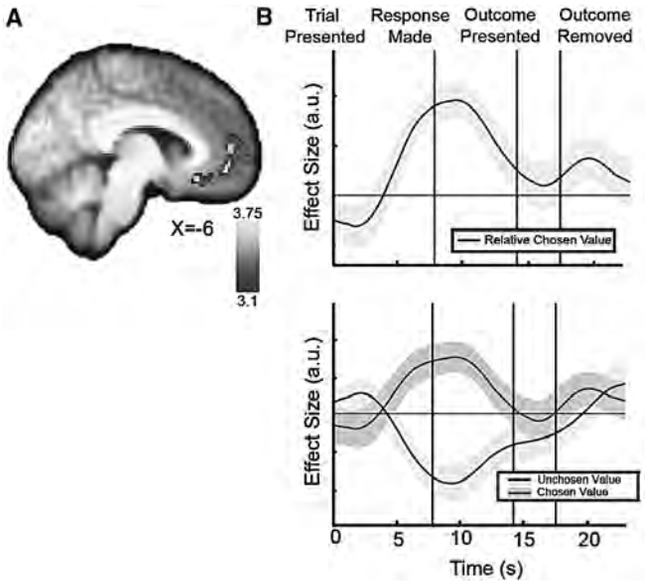

FIGURE 42.2 (A) Sagittal slices through z-statistic maps relating to the relative chosen value (chosen–unchosen expected value) of two options during decision making. (B) *Top panel*: Time course for the effect size of the relative chosen value in the vmPFC is shown throughout the duration of the trial. *Bottom panel*: The same time course is shown with the signal decomposed into chosen and unchosen action values. There is a positive correlation with chosen value and a negative correlation with unchosen value during the decision-making phase. (Adapted from Boorman et al., 2009.)

Some studies, however, have reported slightly different results. For example, Hare, Schultz, Camerer, O'Doherty, and Rangel (2011) reported that vmPFC/mOFC BOLD activity reflected the sum of the values of the choices subjects were offered (rather than the relative difference in their values) while Daw, O'Doherty, Dayan, Seymour, and Dolan (2006) reported vmPFC/mOFC activity reflected the value of the choice that was taken (rather than the difference between it and the rejected option's value).

The time course and emergence of the value difference signal

One way to reconcile these apparently diverging results is to think about them almost as snapshots taken at different time points during the making of the choice. First, the vmPFC/mOFC may represent the value of both potential choices (as in the study by Hare et al., 2011), then it may begin to compare those values, and in the course of doing so a relative value signal will emerge (as in some other studies: Boorman et al., 2009; de Martino et al., 2013; FitzGerald et al., 2009; Philiastides et al., 2010; Wunderlich et al., 2012), and finally, once the comparison process is complete, it is left just carrying a signal representing the value of just the option that has been chosen (as in the study by Daw et al., 2006). This account suggests that if we had a more time-resolved measure of vmPFC/mOFC activity, then we would be able to see the transition from one type of signal to the next.

Hunt and colleagues (2012) tried to take just such a measurement from human subjects during decision making by using magnetoencephalography (MEG) to record brain activity rather than fMRI. First of all, however, Hunt and colleagues attempted to make quantitative predictions about exactly how a neural network ought to make decisions and what signals a network would generate if only the average activity of a brain area, rather than the activity of individual neurons, could be measured. The models they used to predict the activity were first proposed by Wang (2002), and

they employed neuron elements with biophysically plausible properties. Wang's model was originally proposed to explain how neurons in the macaque might mediate choices between one of two eye-movement responses on the basis of graded visual evidence, but it can also be adapted to look at choices made on the basis of different values. At the heart of the model is the idea that the neurons can be assigned to two different pools, each encoding one choice (figure 42.3). Each pool of neurons becomes active in proportion to an input it receives that is, in turn, proportional to the value of the choice it represents. Within a pool of neurons there is recurrent excitatory activity, but the interactions between pools of neurons are mediated by inhibitory interneurons. In essence, this means that each pool becomes active in proportion to the value of the choice it encodes and exerts an inhibitory influence on the other pool that is also proportional to the value of the choice it encodes. Ultimately, the network ends up in one of two possible attractor states in which one pool of neurons is active and the other is not, and this activity pattern constitutes the decision. In general, the pool representing the more valuable of the two options remains active.

When Hunt and colleagues looked at the mean field activity in the model (the sum of the postsynaptic activity throughout the model), they found that it was initially dominated by the sum of the values of the two choice options. Subsequently, the mean field activity reflected the value difference between the choices. They then looked throughout the brains of their human subjects for areas with MEG signals that resembled those they had seen in the model—signals that rose and fell in proportion to, first, the sum of the values of the choices and then the difference in value between choices. They identified two areas with such

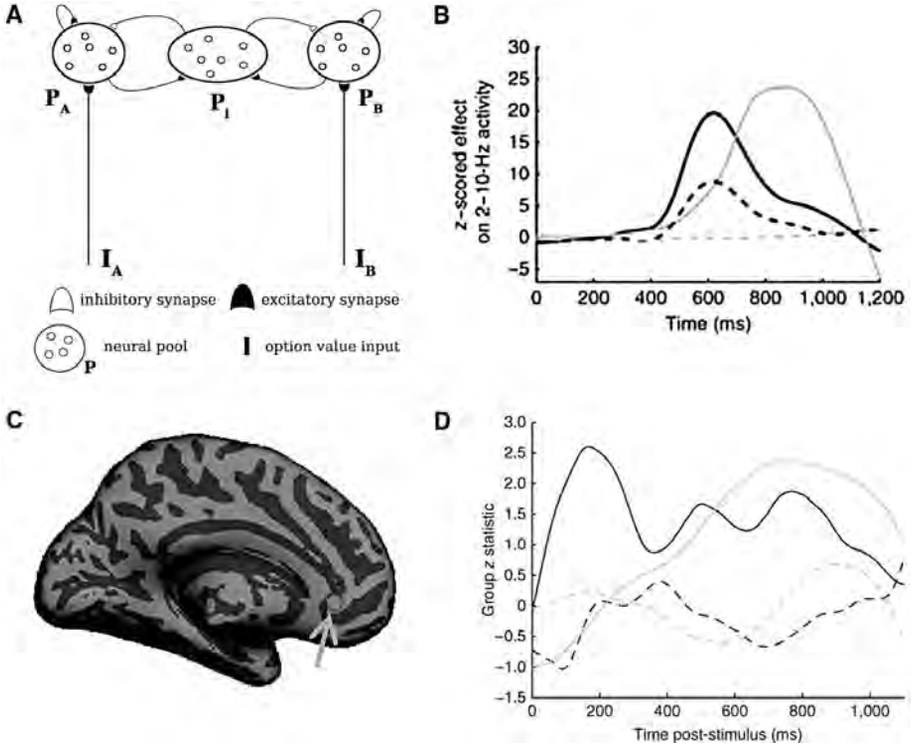

FIGURE 42.3 (A) The biophysical model Hunt and colleagues (2012) used to predict a transition from activity that is proportional to the sum of choice values to the value of the chosen value. It contains two pools of excitatory pyramidal neurons (P_A, P_B) corresponding to choices of either option A or option B. There is recurrent excitation between neurons within pools, but inhibitory interneurons (P_i) mediate competition between pools. Activity in each pool is initially affected by an input proportional (I_A, I_B) to the value of each option, but inhibition between pools leaves only a single pool in a high-firing attractor state. The corresponding option is then chosen. (B) Z-scored effect of overall sum of choice values (on frequency range 3–9 Hz; black lines) and choice value difference (on frequency range 2–4.5 Hz; gray lines) on biophysical model activity; solid lines are correct trials, dashed lines, incorrect trials. (C) vmPFC activity shows several value-related hallmarks of the biophysical network model. (D) Effect of overall value (3–9 Hz; black) and value difference (2–4.5 Hz; gray) on correct/error trials (solid/dashed lines, respectively) during first half of experiment in vmPFC. The analysis used here was performed on human vmPFC but was equivalent to that performed in panel 42.3B on the biophysical model. (Adapted from Hunt et al., 2012.)

signals—one was in the parietal cortex, but the other was in vmPFC/mOFC. In summary, the results are consistent with the idea that a value-comparison process takes place in vmPFC/mOFC, and that during the course of the comparison vmPFC/mOFC is dominated by different types of value signal.

Disrupting vmPFC/mOFC impairs value-guided decision making

If it is true that vmPFC/mOFC discriminates between choices on the basis of their value, then we might expect that vmPFC/mOFC lesions would impair value-guided decision making. We might expect that choice discrimination would become more and more impaired as the difference in choice values decreased. This prediction is based on what happens when mechanisms for color discrimination are impaired by brain lesions in visual association cortex; discrimination performance becomes worse and worse as differences in the color of two stimuli are made smaller and smaller (Buckley, Gaffan, & Murray, 1997).

The prediction was borne out when lesions were made in vmPFC/mOFC in macaques (Noonan et al., 2010). Noonan and colleagues trained their macaques to choose between three stimuli with different probabilistic associations with reward. Each day, the macaques learned about three new stimuli, but on each day one of the stimuli was a high-value stimulus because it was associated with a high probability of reward (0.6), and one stimulus was a low-value stimulus because it had no association with reward (0 probability of reward). The third stimulus was important because on some testing days it was just as poor in value as the worst stimulus (0 probability of reward), but on other days its reward probability began to approach that of the best stimulus (either 0.2 or 0.375 probability of reward). Discriminating the best option from the second-best option therefore became more and more difficult as the second-best option's value approached that of the best option. In the control state macaques were able to make the decision in all three cases, but they learned the identity of the best option more slowly when they were performing testing sessions in which the best option and second-best option were close in value (figure 42.4). Macaques with vmPFC/mOFC lesions were significantly worse when the second-best option was close in value to the best option. In other words, vmPFC/mOFC lesions made macaques worse at taking the most difficult value-guided decisions. Moreover, the disruptive impact on difficult decisions was specific to vmPFC/mOFC lesions and did not occur after lesions in other frontal brain areas that contain neurons with reward-related activity patterns, such as anterior cingulate cortex (ACC) or lateral orbital frontal cortex (lOFC) (Noonan et al., 2010; Rudebeck et al., 2008; Walton, Behrens, Buckley, Rudebeck, & Rushworth, 2010).

Another way to assess value-guided decision making is to examine the consistency and transitivity of choices. Normally, if a person or a monkey prefers option X over Y and Y over Z, then their preferences are said to be transitive if they also prefer X over Z. It is just such transititivity that is lost after vmPFC/mOFC lesions (Rudebeck & Murray, 2011). Once again, the effect is specific to vmPFC/mOFC lesions and is not seen after lOFC lesions. Similar patterns of impairment in value-guided decision making have also been reported in human patients with vmPFC/mOFC lesions (Camille,

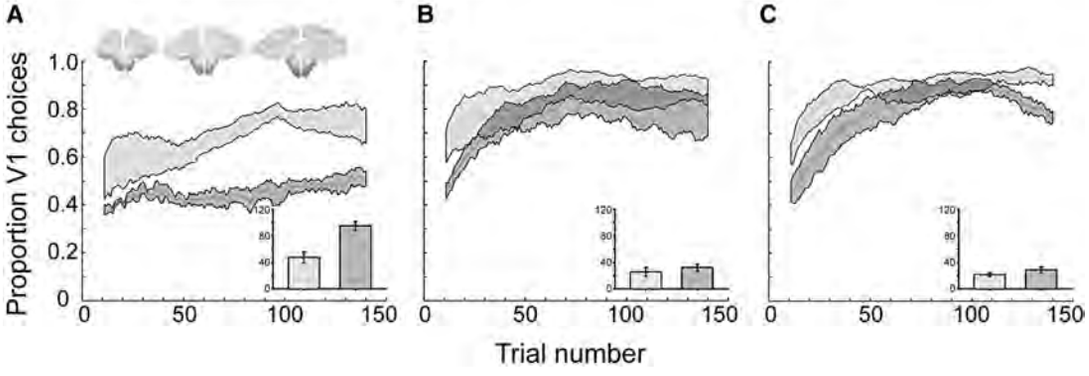

Figure 42.4 Effect of choice option value proximity for macaques with mOFC lesions. Proportion of choices which were of the best value option when the difference in value between the best and second-best option was small (A, 0.2), medium (B, 0.4) and large (C, 0.6). Control pre-lesion (light gray), post-mOFC lesion (dark gray) performance. Insets show number of trials to reach 70% V1 choices. Lesions of mOFCs caused impairments when the best and second-best value differences were small (A). The mOFC lesion locations are represented on an unoperated control brain, with darkness indicating lesion overlap (overlap in one to four animals). (Adapted from Noonan et al., 2010.)

Griffiths, Vo, Fellows, & Kable, 2011; Fellows, 2011; Henri-Bhargava, Simioni, & Fellows, 2012).

The activity of neurons in vmPFC/mOFC

Despite the abundance of neuroimaging studies of vmPFC/mOFC, we have relatively little knowledge of this region's activity at the level of individual neurons. A handful of very recent studies have reported that the activity of neurons in the vmPFC/mOFC of the macaque is modulated when there is a possibility that a reward rather than a punishment might be received (Monosov & Hikosaka, 2012). Firing rate is modulated as a function of the reward size (Bouret & Richmond, 2010; Kaping, Vinck, Hutchison, Everling, & Womelsdorf, 2011) and reward probability (Monosov & Hikosaka, 2012) that is associated with a stimulus that is chosen.

What is less clear is quite how vmPFC/mOFC activity evolves during the course of a decision. Padoa-Schioppa and colleauges (Padoa-Schioppa, 2009; Padoa-Schioppa & Assad, 2006) have presented a detailed account of single-neuron activity patterns when macaques choose between different amounts and types of rewards. In a number of ways, the activity is reminescent of the MEG signals reported by Hunt and colleagues (2012) because it is, initially, related to the value of the potential choices that might be taken. This signal is then rapidly followed by another pattern of activity that is related to the value of the choice that is actually being taken. However, the region in which recordings were made is probably just lateral to the one that has been the focus of the neuroimaging and lesion studies of reward-guided decision making and probably lies in lOFC. Despite the important differences between vmPFC/mOFC and lOFC and their anatomical separation, there are interconnections between the two regions (Carmichael & Price, 1996).

Translating values into actions: Integration across frontal lobe systems

When vmPFC/mOFC makes a decision, it does not do so in the sense of choosing a specific action, but instead the type of decision that it makes is the selection of a reward goal that becomes the focus of behavior. This appears to be especially the case when there are multiple competing alternative choices and attention must be directed while critical comparisons are made between the various options (Noonan et al., 2010). Once the reward goal is selected, then a second type of decision has to be made about which action should be made to obtain the reward goal.

There was little evidence in OFC of encoding of the actions that monkeys made when they were choosing between different types and amounts of reward (Cai & Padoa-Schioppa, 2012; Padoa-Schioppa & Assad, 2006). By contrast, when ACC neurons are recorded in the same paradigm, they do not encode the values of the potential choices, but they do encode the value of the choice taken, and do so with a longer latency than OFC neurons (Cai & Padoa-Schioppa, 2012). ACC neurons did, however, encode the direction of the action used to affect the choice. In other words, it seems that, at least in the paradigm studied by Padoa-Schioppa and colleagues, ACC neurons are only encoding the output of a decision process rather than the decision itself, but that they are then encoding features of the action that will be used to make the choice. Some human neuroimaging studies might be interpreted in a similar manner (Noonan, Mars, & Rushworth, 2011).

The ACC region that carried both chosen value and action direction signals is well placed to influence the motor system. It lies on the dorsal bank of the cingulate sulcus and it is adjacent and interconnected with a region called the rostral cingulate motor area (van Hoesen, Morecraft, & Vogt, 1993). The rostral cingulate motor area in turn sends projections to the spinal cord that probably allow it to influence movement in a relatively direct manner (Dum & Strick, 1991; He, Dum, & Strick, 1995).

In summary, one way in which different frontal lobe areas might interact during decision making is for vmPFC/mOFC and possibly adjacent OFC areas to make a choice between different possible reward goals and for ACC to decide between different possible actions. It is, however, important to emphasize that in the experiments of Padoa-Schioppa and colleagues the only meaningful associations with reward are with stimuli. A given stimulus appears at different locations on different trials, so that the actions that are made to select the stimulus change from trial to trial and actions made to particular locations do not have a consistent relationship with a reward if the stimulus at that location changes. It is possible that another role for the ACC might be revealed if the animals are given the opportunity to learn direct associations between actions and rewards that do not involve any mediation by visual stimuli. Rudebeck and colleagues (2008) and Luk and Wallis (2013) taught macaques tasks in which associations had to be learned between actions and rewards in the absence of any mediating stimuli, and compared them with the more commonly studied type of task in which macaques learned associations between stimuli and rewards. More ACC neurons encoded the choices animals made when they were performing the action-reward association task than the stimulus-reward association task, whereas the opposite was true in lOFC

(Luk & Wallis, 2013). ACC lesions impaired action-reward association learning but not stimulus-reward association learning, while the opposite was true after lOFC lesions (Rudebeck et al., 2008). A similar dissociation between the effects of ACC and OFC lesion deficits has been reported in human patients (Camille, Tsuchida, & Fellows, 2011).

Such patterns of neural activity and lesion effects suggest the existence of different mechanisms for decision making in ACC versus vmPFC/mOFC and lOFC. It is possible that these different mechanisms work in a completely parallel manner, with one set of brain regions learning associations between actions and rewards and another set learning associations between stimuli and rewards. However, it seems unlikely that this will be the case. While values may adhere to particular stimuli and objects in the world in a relatively constant fashion, it is not clear that this is always likely to be true of actions. For example, the value of an action directed to the left or the right might, in many real-world scenarios, change depending on which way a person is facing. What might, however, be pertinent for a system that can bring together information about reward and actions is to decide whether it is worth persisting with a given action or whether it might be better to try an alternative one. These are the types of decisions that animals often have to make when there are no specific stimulus-reward associations available to guide their behavior. In addition, it might be useful for such a mechanism to compute whether the effort entailed by an action outweighs the benefit that it bestows. The next section considers such possibilities in the context of the foraging choices that are important for many animals.

Distinct mechanisms for decision making in ACC and vmPFC/mOFC

The last section discussed how vmPFC/mOFC might be a mechanism for making decisions between potential choices. Although such decisions are commonly studied by psychologists, cognitive neuroscientists, and economists, they may be surprisingly rare outside of the laboratory. This is simply because in many natural situations, when an animal is foraging, potential food items are encountered sequentially rather simultaneously (Freidin & Kacelnik, 2011). It might be only on some occasions that a macaque foraging in the wild is given the opportunity to make the type of choice that the vmPFC/mOFC appears to make—for example, a choice between an apple and an orange. Instead, what is more likely to happen is that the macaque might first see an opportunity to pursue a course of action that might lead to one piece of fruit and only later perceive the opportunity to pursue another piece of fruit by taking another course of action. The critical choice for the foraging animal is, therefore, whether to *engage* with a potential food option or whether to carry on *searching* for better opportunities elsewhere.

In contrast to cognitive neuroscientists, behavioral ecologists have long been interested in such choices. Whether or not an animal engages with the potential option it encounters is determined by the value of the encountered option, the effort that will be expended in engaging with it, whether the environment is, on average, sufficiently rich that better options are likely to be encountered frequently if the animal carries on searching, and how effortful it will be to continue searching (Charnov, 1976; Stephens & Krebs, 1986). In summary, foraging decisions should be governed by the average value of continuing to search (*search value*), the effort entailed by searching (*search costs*), and the value of each option encountered (*encounter value*). Despite the ecological importance of such choices, surprisingly little has been known about their neural mechanisms.

Kolling, Behrens, Mars, and Rushworth (2012) attempted to compare the neural processes underlying engage/search foraging choices with the neural mechanisms underlying binary decision making. On each trial, human subjects could alternate between two different styles of decision making while fMRI data were collected. Before the subjects entered the scanner, they had learned about a set of visual stimuli in which each stimulus was associated with a different number of points that were translated into a monetary payment at the end of the trial. At the beginning of each trial in the fMRI experiment, subjects saw two of these stimuli (figure 42.5). The options encountered in this way were referred to as the *encounter* options. They were intended to simulate the opportunity that a foraging animal might engage with. The investigators refered to their values as *encounter values*. A box at the top of the screen included a number of alternative stimuli. These were intended to represent the richness of the subject's current foraging environment and to indicate the *search value*; if the subject did not engage with the encountered option, then he or she opted to search for better options that would be drawn at random from the stimuli in the box and become the encounter options on the next trial. The first decision that subjects made on each trial was therefore a foraging-style choice to either engage with an encountered option or to search for better alternatives. To simulate search cost, subjects lost points if they chose to search (the cost on each trial was indicated by the color of the box surrounding the search options). Subjects could keep opting to search

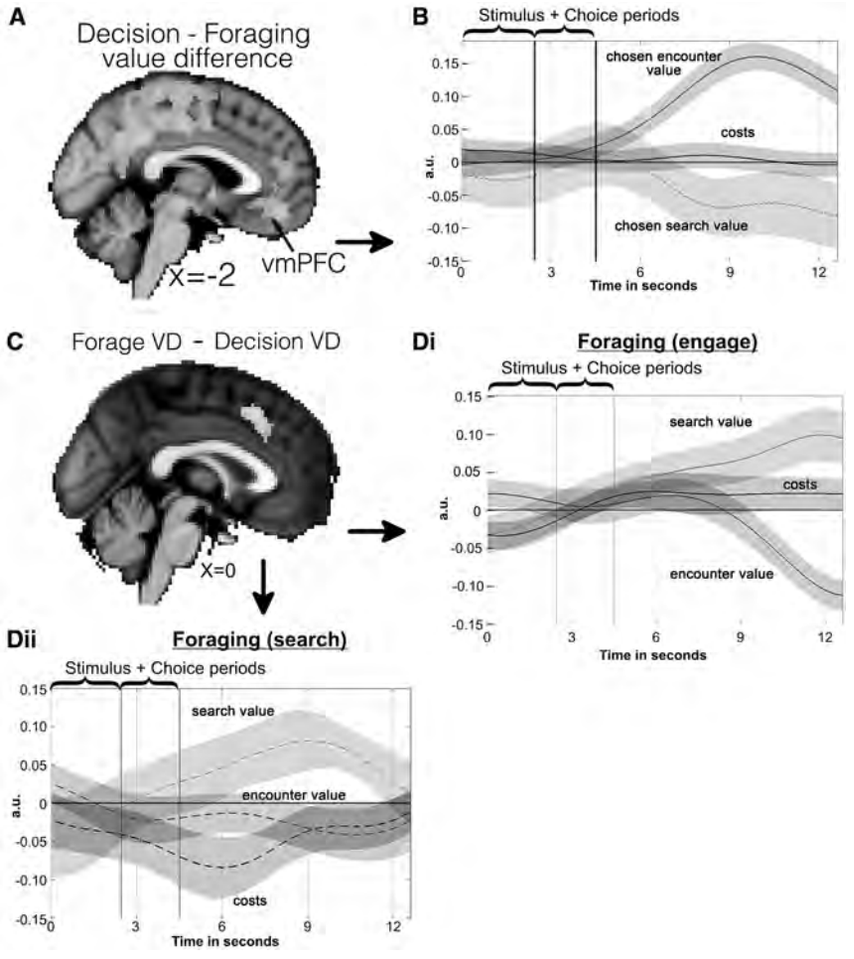

FIGURE 42.5 While vmPFC/mOFC is more active during decision making than foraging (A, B), an ACC region is more active during foraging than decision making (C). The ACC BOLD is positively correlated with the search value and negatively correlated with the encounter value regardless of whether subjects choose to stick with the option encountered (Di) or to search for potential alternatives when the search cost is also represented (Dii). By contrast, vmPFC/mOFC BOLD is positively correlated with the encounter value, when it is chosen, but there is no representation of search values or costs regardless of the choice ultimately made (B). (Adapted from Kolling et al., 2012.)

for better alternatives as many times as they wanted. However, as soon as they opted to engage, they were then able to make the second type of decision—a binary comparitive decision between the two component stimuli that constituted the encounter option. This second decision was therefore of the same type as those that are known to be related to the vmPFC/mOFC.

Several aspects of the results suggested binary choices and foraging choices were being mediated by the vmPFC/mOFC and the ACC, respectively. First, several brain areas, including ACC, were more active when subjects made foraging-style engage/search choices, while other brain regions, including vmPFC/mOFC, were more active when subjects made binary comparison decisions (figure 42.5). Perhaps even more importantly, ACC activity reflected all three key factors that should determine foraging: encounter values, search values, and search costs. By contrast, vmPFC/mOFC only carried an encounter value signal but no representations of search value or search costs. Other fMRI experiments have also reported integrated reward/effort signals in ACC as opposed to vmPFC (Croxson, Walton, O'Reilly, Behrens, & Rushworth, 2009).

Another reason for thinking the two regions, vmPFC/mOFC and ACC, were mediating binary comparative decisions and foraging choices, respectively, could be found in examination of individual differences in activity patterns in the two regions. Individual differences in the strength of ACC signals, but not vmPFC signals, were correlated with individual differences in foraging behavior. Individual differences in the strength of vmPFC/mOFC signals, but not ACC signals, were correlated with individual differences in the way binary comparative choices were made.

The way in which ACC encoded values for foraging choices was quite distinct from the manner in which vmPFC/mOFC encoded values during binary decision making. As earlier sections have described, vmPFC/mOFC encodes a relative value difference signal, with the BOLD signal increasing as a function of the value of the chosen option and decreasing as a function of the value of the rejected option. By contrast, rather than encoding decision values in a framework that is relative to the choice that is made, the ACC encodes foraging choice values in a fixed manner; ACC activity always increases as a function of the search value and decreases as a function of the encounter value. The search value signal, however, ramps up more quickly when subjects are going to make the search choice rather than the engage choice (figure 42.5).

In the foraging task it was noticeable that by default subjects often seemed simply to engage with the option placed in front of them; subjects made more of these choices and did not move away from them unless the value of searching considerably outweighed the value of engaging. One way of thinking about the ACC's choice signals is that they are configured in such a way as to indicate the value of changing away from the current default behavior and of searching for better alternatives.

Reinterpreting the role of ACC

The hypothesis that ACC encodes value signals that are needed for foraging-style choices can explain some of the other signals that have been reported in ACC in the past. For example, it has been noted that during binary choices the ACC often carries a signal that is inversely proportional to the difference in value between the choices available, rather than proportional to the differences in value between the choices as in vmPFC/mOFC (Hare et al., 2011). According to the foraging hypothesis, the inverse value signal recorded during a binary comparison task can be interpreted as a signal reporting how beneficial it would be to not take the choice that is about to be taken but, instead, to switch to the other choice.

Another important strand of research has linked ACC to detecting when there is conflict between possible responses that might be made (Botvinick, 2007). Response conflict occurs when there is a similar amount of evidence favoring more than one response, and once again the ACC may be signaling the value of taking a course of action that is alternative to the one that is being taken. It is not clear, however, that a theory that focuses just on conflict monitoring could explain some of the results found in the foraging task.

If ACC has a mechanism for valuation and promotion of behavioral change and search, then this may suggest a reinterpretation of some other findings made during earlier investigations of ACC. The action-reward learning tasks that are impaired by ACC lesions (Camille, Tsuchida et al., 2011; Kennerley, Walton, Behrens, Buckley, & Rushworth, 2006; Rudebeck et al., 2008) typically involve alternation between actions but no informative stimuli. Repetitive selection of an action interleaved with periods of exploration of alternative actions may be just the sort of behavior normally under the control of a foraging system. It may be that the ACC lesion did not disrupt a mechanism for linking specific actions to outcomes but that, instead, it disrupted a mechanism with which animals decide whether to persist with one choice versus switching to an alternative.

The human ACC region that carries search/engage signals for foraging is well placed to influence whether or not a successful action will be repeated or whether the value of an alternative action will be explored. It lies just adjacent and anterior to the human rostral cingulate motor area (Amiez & Petrides, 2014; Beckmann, Johansen-Berg, & Rushworth, 2009; Picard & Strick, 1996), and as we have already seen a similar region is interconnected with the rostral cingulate motor area (van Hoesen et al., 1993), which has connections to a number of motor regions.

ACC neurons during searching and foraging

A longstanding problem that has dogged attempts to understand ACC has been the difficulty of finding single-neuron activity patterns that are consistent with some of the most influential theories of ACC function. For example, it has proven difficult to identify ACC neurons that detect conflict (Nakamura, Roesch, & Olson, 2005). By contrast, there are several reports of ACC neuron activity that suggest that it is concerned with searching the environment for the best choices to take and with foraging-style search/engage decisions.

Quilodran, Rothé, and Procyk (2008) taught macaques a task in which they had to work out which one of four options was associated with reward. The macaques solved the task by searching through each of the four possible choices. When they identified the choice that was associated with reward, they were allowed to repeat it again for several trials and received rewards on each occasion. After several trials, however, the reward was reassigned to another option and the cycle of searching for the best option, and then repeatedly choosing that option, began again. The animals,

therefore, alternated between periods of searching for good choices to take and, once a good choice was identified, of exploiting that choice by taking it repeatedly. The firing rate of many ACC neurons was modulated when the outcomes of the choices were revealed to the monkeys in the search phase of the task, and this was apparent both when the choice led to nonreward as well as when it led, for the first time, to a reward (the first reward, of course, defined the end of the search period). As the monkey shifted into the repetition phase of the task, however, ACC neuron outcome-related activity diminished and instead activity became more prominent at the moment that choices were reinitiated (figure 42.6).

Other features of ACC activity also attest to the importance of the transition between searching and repetitive behavior. Both nonreward and reward outcomes in the search period were followed by an increase in high gamma (60–140 Hz) power in the ACC, which was then followed by a similar increase in lateral prefrontal cortex (Rothé, Quilodran, Sallet, & Procyk, 2011). By contrast, in the repetition phase, post-choice outcome-related activity in ACC and lateral prefrontal cortex was correlated in the beta (10–20 Hz) band.

Other experiments have made even more explicit attempts to simulate the type of foraging decision that animals have to make in the wild. Hayden, Pearson, and Platt (2011) designed a laboratory task for macaques that simulated the types of foraging choices that are considered by Charnov's (1976) marginal value theorem. The marginal value theorem was proposed to explain how animals should spend their time in an environment composed of patchily distributed food sources. As an animal forages in its patch, it gradually depletes the resources it contains. For example, a monkey that continued to forage in the same tree all the time would gradually deplete the fruit it contained. In a patchy environment, an animal should continue foraging within its patch for longer when that patch is richer in resources than the average patch or if considerable effort is going to have to be invested in traveling a large distance to the next patch. Hayden and colleagues simulated such a situation by giving their macaques a target to which they could saccade in order to indicate they wanted to remain foraging in the same patch. Each time they made this decision they received a reward, but the reward gradually declined in size just as the returns from a food patch in the wild might decline if it is continually exploited. The macaques could indicate that they wanted to leave the patch by saccading to another stimulus. There was then a delay until they had their next chance of reward (the delay simulates travel time to the next patch), but the reward level in the new patch was high (this simulates how the new patch has not yet been depleted).

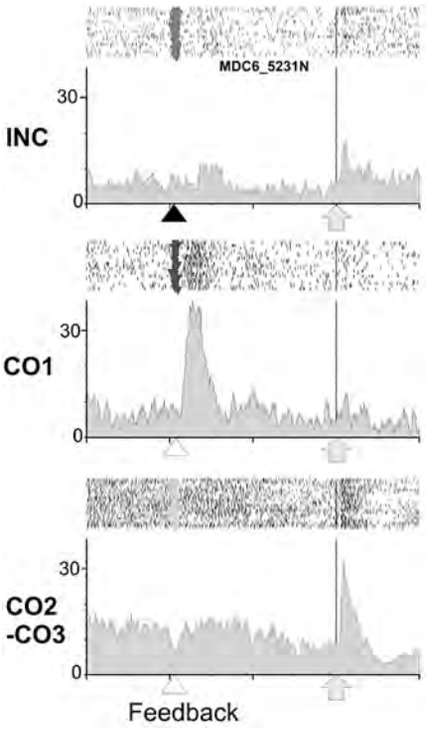

Figure 42.6 Macaque monkeys were taught to identify which of four possible directions of response was the correct one. The correct direction remained the same for a few trials but then changed. In this example, there is an increase in activity after feedback (indicated by arrow head) informs the monkey that the action just made is now correct and reward is delivered, but this occurred only on the first occasion that the action was established as the correct one (CO1, second row) and not on subsequent trials (bottom row). This neuron also indicated the direction or sign of the change in action value; it was active when the action was rewarded for the first time, but not when an exploratory choice established that the action was not rewarded (INC, top row). Other neurons exhibited the opposite pattern of activity. Once the action is established as rewarding, the ACC activity occurs in expectation of reward at the time that the lever is touched (vertical line), rather than at the time of feedback (CO2-CO3, bottom row). In other words, ACC activity contains information both about action value expectations and errors in predictions when actions were better or worse than expected. Each row of the figure shows both raster diagrams of the action potentials recorded on individual trials at the top and the mean frequency of action potentials at the bottom. (Adapted from Quilodran et al., 2008.)

The pattern of results suggested that ACC neurons were monitoring the reward intake rate in the current patch and contributing to the monkeys' decisions to leave the patches (figure 42.7). ACC neurons were active in response to the delivery of rewards received each time the monkey carried on foraging in its patch,

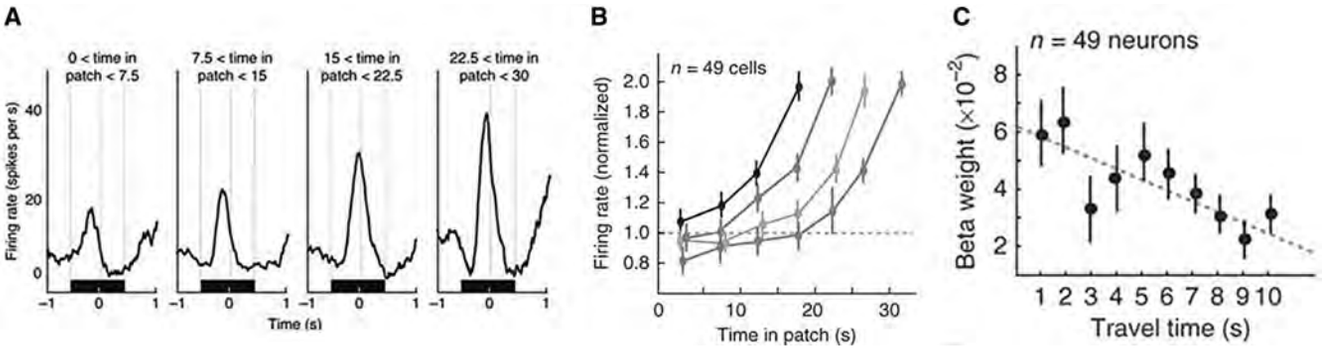

FIGURE 42.7 The activity of neurons in ACC in monkeys during a foraging task. Outcome-related activity increases with each outcome that is received for foraging in a given patch in an example neuron (A) and, on average, the gain of the outcome-related response with time in the patch co-varied with the speed of departure from the patch (B). The rate of gain was a function of the search costs that were to be paid; here, rate of gain is indicated by a regression slope (beta weight) relating time spent foraging in a patch with firing rate, and it can be seen that it decreases with the search cost that will have to be paid in order to travel to a new patch. (Adapted from Hayden et al., 2011.)

but the reward-related firing rates gradually increased as the time approached for the patch-leaving decision. After the reward-related firing rate reached a certain level, the monkeys tended to switch to a new patch on the next trial. The steepest rises in firing rates were seen on those trials where the animal left the patch soonest and when the travel time to the next patch was shortest.

A more direct demonstration that ACC neurons might integrate information, not just about reward expectations, but also about the effort that is going to be invested in pursuing a course of action comes from a multidimensional choice task that involved macaques making choices between different pictures that were each associated with different outcomes (Kennerley, Dahmubed, Lara, & Wallis, 2009). The three critical dimensions that defined each outcome were the size of reward payoff (volume of juice delivered), effort (number of lever presses necessary to earn the reward), and the probability (probability that reward would be delivered). Kennerley and colleagues found that neurons in all three areas they investigated, ACC, lOFC, and lateral prefrontal cortex, encoded the three different factors that determined choice values. However, ACC neurons more frequently encoded each of the three value-determining factors than did lOFC or lateral prefrontal neurons. Individual ACC neurons were also especially likely to multiplex information across all three value dimensions so that information about, for example, both the reward benefits and the effort costs of a choice was integrated within the firing rate of single ACC neurons. Such activity patterns might underlie the integration of reward/effort expectations in ACC activity reported in fMRI studies (Croxson et al., 2009) and would, of course, enable ACC to make the type of reward benefit/effort cost decisions that have been associated with ACC activity (Kolling et al., 2012).

Lesion studies also suggest ACC plays a critical role in integrating information about reward and effort expectations during decision making. Rats can be trained to make choices between two arms of a T-maze that are associated with different reward benefits (for example, two versus four reward pellets) and different effort costs (such as climbing over a barrier versus no barrier). Normally rats are prepared to pay some cost in order to receive a bigger reward benefit, but this changes after lesions are made in the Cg1/Cg2 fields of the ACC (Rudebeck, Walton, Smyth, Bannerman, & Rushworth, 2006; Schweimer & Hauber, 2005; Schweimer, Saft, & Hauber, 2005; Walton, Bannerman, Alterescu, & Rushworth, 2003; Walton, Bannerman, & Rushworth, 2002; Walton et al., 2009). By contrast, lesions of orbitofrontal cortex or prelimbic cortex, in the rat, do not have the same effect.

Conclusion

We have emphasized the different functional contributions of frontal lobe regions to value-guided decision making. We have emphasized a flexible vmPFC/mOFC system that makes comparisons between choice values by focusing on the most relevant aspects of value (for example, reward probability or reward magnitude). In some cases such a system may work in series with brain areas such as the ACC, which might select an action compatible with the reward goal that is the focus of attention. In some situations, however, the ACC might operate in a quite independent manner to take simple stay-switch decisions on the basis of different types of value information such as average search values and

effort costs. Although such decisions have received comparatively little attention from cognitive neuroscientists, they may be just the sort of decisions that many animals make when they are foraging, and they may be the types of decisions that many brain regions have evolved to take.

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