NEURAL BASIS OF DECIDING, CHOOSING AND ACTING

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The ability and opportunity to make decisions and carry out effective actions in pursuit of goals is central to intelligent life. Recent research has provided significant new insights into how the brain arrives at decisions, makes choices, and produces and evaluates the consequences of actions. In fact, by monitoring or manipulating specific neurons, certain choices can now be predicted or manipulated.

Movements of physical bodies, such as rocks, are explained by external forces. Such external factors are referred to as 'causes'. By contrast, many human movements are distinguished from the movements of rocks by having explanations in terms of not just causes but 'reasons'. We describe human movements as 'actions' directed towards a goal for a purpose, and not just as 'events' that happen through a more or less complex chain of causes. Explaining my typing of these words entirely in terms of a pattern of neural activity in my spinal cord, which produces muscle contractions in my fingers so that a keyboard is hit in a particular pattern, seems incomplete. A more satisfying explanation would include reasons, desires and plans – such as "I want you to know this".

A fundamental goal of cognitive neuroscience is to understand how mental entities like 'reasons' and 'desires' derive from processes in the brain. But as we come to understand the internal factors of human action in terms of brain function, we must confront the fact that the brain comprises neurons and glia that fundamentally have no interests. To paraphrase Wittgenstein, what, if anything, is left if we subtract brain processes and associated body movements 'happening' from the agent 'acting'? To answer this question, we must understand the basic properties of decisions, choices and actions, and how they arise from brain processes. We are beginning to reach such a level of understanding of how the brain makes decisions and generates actions. This review will emphasize findings obtained in experiments in which the activity of individual neurons was monitored in specific parts of the

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brain of highly trained macaque monkeys performing certain tasks. The tasks typically presented monkeys with a stimulus or set of stimuli that required some interpretation to determine which of two or more behavioural responses to produce to receive a juice reward. Although these are rudimentary tasks compared with human decision making under more complex conditions of risks, uncertainty and deadlines[1], we can be optimistic that the information gained from these initial neurophysiological studies will provide a foundation for future experiments that investigate more complex decisions.

Choices, decisions and actions

The recent literature in cognitive neuroscience refers to human and nonhuman subjects as 'deciding', 'attending', 'intending', and so on. When a neurophysiologist uses these words, does he mean the same thing as a philosopher, a lawyer, or the man on the street? If we are to understand the neural mechanisms of decision, choice and action, then we must use precise and effective definitions that are consistent with both the casual and technical meanings. I will discuss the operational definitions of these terms, which are derived from philosophical sources[2–4].

Choice. A choice is required when an organism is confronted with alternatives for which an action is necessary to acquire or avoid one or more of the alternatives because of a desire, goal or preference. An effective definition is that a choice at the most fundamental level is an overt action performed in the context of alternatives
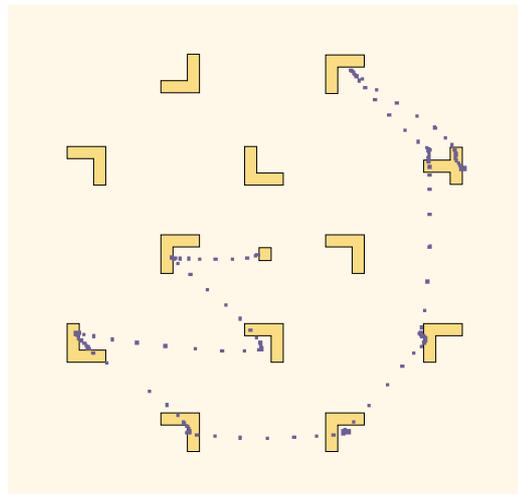
Figure 1 | **Visual choice behaviour.** The pattern of gaze shifts made by a monkey searching for a randomly orientated T among randomly orientated Ls. The visual array appeared after the monkey had fixated the central spot. In this trial the monkey's first eye movement was to the left, followed by a gaze shift to the element below the fixation spot, followed by a sequence of eye movements around the perimeter of the array. The T was fixated briefly before an eye movement to another L stimulus, followed shortly by an eye movement back to the T. This simple behaviour allows investigators to ask questions such as: What processes in the brain led to the particular movements that were made? How did the brain control when to move the eyes? How did the brain identify and correct the errant eye movement past the T target? (Figure modified with permission from REF. 9, taken from the *Annual Review of Neuroscience*, Volume 22 © (1999) by Annual Reviews www.AnnualReviews.org.)

for which explanations in terms of purposes can be given. Ordering a meal at a restaurant is an example of a choice. You may or may not need to deliberate about which meal you prefer, but you must indicate your choice through some action like speaking or pointing at one of the options on the menu.

Movements of the eyes are another kind of action that can be made in the context of alternatives for a purpose (FIG. 1). Most visual images, especially natural scenes, present a multitude of alternative targets for fixation among which just one can be examined at a time. Visually guided eye movements have been a very effective behaviour with which to address issues about perception, cognition and choice behaviour[5]. Choices take time; a choice process evolves from a state of more or less equipotentiality immediately after the alternatives are presented to a state of commitment before the overt action is performed. With prior knowledge of the alternatives and preferences, choices can be predicted.

Decision. We should start by distinguishing 'decide to' from 'decide that'; this review is about 'decide to'. The fact that choices can be predicted means that it is possible to choose in advance — "I will have the Blue Plate special when we get to the restaurant". This sense of choice approximates decision; however, important distinctions should be recognized between choice and

decision. Foremost, whereas choice refers to the final commitment to one alternative, decision refers to the preceding deliberation about the alternatives.

The polarity of deciding and choosing can be highlighted by considering a visit to a new restaurant. Everyone must enact a choice, even those who have frequented the restaurant. But if the restaurant is new to you, then before you can choose (produce one of many possible overt actions with the purpose of communicating which meal you wish to receive), you must learn the alternatives, understand the differences between them and how they relate to your preferences, and deliberate about which would be most satisfying. A defining feature of decisions that distinguishes them from choices is that decisions cannot be predicted — even by the agent. If you can say what you will decide, then you will have decided. A corollary of this is that decisions, like perceptions, seem just to happen; introspection cannot find the source of the decision[6].

Action. The definition of an action is a complex issue[7]. Often one does one thing (order a meal) by doing something else (point at the menu). But to point at the menu, one must do something else (move a finger). A 'basic action' is an action we perform without any preliminaries, such as moving a finger. We cannot say how we move our finger; it just happens when we will it. Defining a body movement as an action depends on context. A purposeful action (pointing at the menu) is distinguished from a mere event (a hand jostled by a passing waiter) by reference to some intelligible plan. Actions are performed to achieve a goal.

Neurophysiologists have made considerable progress in characterizing the brain processes that occur when nonhuman primates make decisions and choose among alternatives by producing specific movements with the purpose of earning a reward[8–11]. This review is concerned with how neural activity relates to the decisions, choices and actions of monkeys. For an overview of the structures of the brain that are implicated in choices, decisions and actions, see BOX 1.

Neural correlates of choosing

The visual search paradigm has been used extensively to investigate visually guided choice behaviour[12]. In a visual search task, a target stimulus must be discriminated from an array of distractor stimuli. Visual search for a single target among distinct alternatives, known as 'feature search', requires a choice that can be based entirely on sensory processing. Search is more efficient if the target is conspicuously different from distractors — for example, a different colour or shape. Search is less efficient if the target is less discriminable from distractors — for example, a small difference in colour or shape, or shared features in a search for a conjunction of features. Several laboratories have investigated how the visual system selects the conspicuous stimulus in an image[13–17]. For example, in the FRONTAL EYE FIELD of monkeys trained to shift gaze to the target in a visual search array to earn a reward, visually responsive neurons initially respond indiscriminately to the target or the distractor of the

FRONTAL EYE FIELD
An area in the frontal lobe that receives visual inputs and produces movements of the eye.

Box 1 | **Organization of sensorimotor systems**

Neural concomitants of deciding, choosing and producing actions occur in numerous areas of the cerebral cortex, not to mention the subcortical structures. This box provides a simplified perspective of the brain regions described in the text.

Vision starts in the retina and is fulfilled in the cerebral cortex. Visual processing in the cortex starts in the primary visual area (area V1). Neurons in V1 have small receptive fields in a very precise topographic map of the visual field; they respond preferentially to stimuli of different orientation, colour, direction of motion, stereoscopic depth, and so on. Outputs from the primary visual cortex innervate secondary and tertiary areas that project to other visual areas in the parietal and temporal lobes.

The connections between visual areas form a complex network that is organized into two main streams. One stream passes into inferior temporal (IT) cortex. Neurons in caudal IT cortex are tuned for stimulus features such as colour or shape; neurons in rostral IT cortex are selective for more complex visual objects such as faces. The second cortical visual processing stream passes through the middle temporal (MT; also referred to as V5) visual area into posterior parietal cortex. Neurons in area MT respond best to stimuli moving in one direction. Neurons in posterior parietal cortex exhibit two pronounced extra-retinal signals: the first is a modulation of visual responses related to orientating to stimuli; the second is a modulation of visual responses by the angle of gaze.

Visual processing is not completed in the parietal and temporal end stations of the two streams. Signals are conveyed from posterior parietal cortex and inferior temporal cortex to prefrontal cortex, the function of which is less understood but involves organizing actions over extended periods. Two areas about which much is known are dorsolateral prefrontal area 46 and the frontal eye field. The processing subserved by area 46 has been characterized as working memory or as mediating the linkage across time of stimulus and response. The frontal eye field represents the stage of visual processing at which the location of salient stimuli becomes explicit and the command to orientate is produced. Neural activity associated with visually guided eye movements is also found in the supplementary eye field, but hypotheses about the function of this cortical area have also included self-generated saccade production, conditional motor learning, object perception and more recently behaviour monitoring.

Vision during a period of fixation culminates in another eye movement. A network located in the brainstem is responsible for generating saccadic eye movements. The saccade generation network requires two conjoint inputs: one signalling the desired direction and amplitude of the movement; the other signalling when to initiate the movement. A main source of these signals is the superior colliculus, which receives visual inputs from the retina as well as descending inputs from many cortical areas, in particular the posterior parietal cortex, the frontal eye field and the supplementary eye field. Electrical stimulation has been used for over a century to map the parts of the brain that produce movements of the body. For example, electrical stimulation of brain structures that generate the command to shift gaze, such as the frontal eye field or the superior colliculus, elicits an eye movement if the current and frequency are high enough.

Cortical tactile processing begins in postcentral somatosensory cortex. Limb movement follows activation in agranular frontal cortex, which is divided into primary motor cortex, premotor cortex and the supplementary motor area. Primary motor cortex is the origin of the principal innervation of the spinal cord necessary to produce movements. Premotor cortex and the supplementary motor area subserve movements that are more complex, or generated in response to arbitrary stimulus cues or internal states.

ODDBALL
The one stimulus that is different from all of the rest. Usually refers to the stimulus that has a unique feature (colour, form, direction of motion) in a visual search array.

search array in their receptive field. Then the neural activity evolves to signal the location of the target stimulus before the eye movement to the target[18,19] (FIG. 2a). Complementary observations have been made in monkeys scanning complex images[20].

Does this neural selection require an overt eye movement? To address this question, the activity of neurons in the frontal eye field was recorded while monkeys maintained fixation during presentation of the visual array with one ODDBALL[21]. Although no eye movement was made, the neurons in the frontal eye field still dis-

criminated the oddball from distractors (FIG. 2b). One interpretation of this observation is that the selection happened automatically, so the choice was effortless. In fact, preliminary evidence shows that this visual selection can occur even if the monkey's gaze shifts to a location other than that occupied by the oddball[22]. These findings are consistent with the fact that we can choose in advance; in other words, we can achieve a cognitive state that specifies a particular alternative even though the overt action that signifies the selection of that alternative need not have been produced.

Neural correlates of deciding

A decision process precedes choices that involve some perplexity, that is, when the alternatives are difficult to distinguish, have uncertain pay-offs or require prior knowledge to resolve them. Thus, in contrast to simple choices, decisions are more effortful, take more time, require attention and deliberation, and are more error prone.

Decisions requiring knowledge. Visual search for a target defined by a conjunction of features requires sensory processing supplemented by top-down knowledge[12]. In monkeys performing visual search for a target defined by a combination of colour and shape (conjunction feature search), two top-down influences on gaze behaviour and the neural selection process have been observed[23]. First, an influence of visual similarity was revealed by occasional errant gaze shifts to those distractors that resembled the current target. The same influence has been observed in humans[24–26]. This influence was evident in the activity of neurons. When the monkeys shifted gaze successfully to the target, frontal eye field neurons not only discriminated the target from the distractors, but also discriminated among the non-selected distractors, producing more activation for distractors that shared a feature with the target than for the distractor that did not (FIG. 2c).

The second influence was derived from the history of stimulus presentation across sessions. In error trials, monkeys showed a tendency (in addition to the visual similarity tendency just described) to shift their gaze to the distractor that had been the target in the previous session. In correspondence to the behaviour, in trials when the correct eye movement was made to the conjunction target, distractors that had been the search target during the previous session were represented by stronger activation than were the other distractors[23]. The pattern of neural discrimination among non-selected distractors corresponded to the pattern of errors, showing the combined influence of sensory properties and experience on the neural representation of the alternatives that leads to a particular pattern of choices. This observation is consistent with other studies showing that neural activity in various frontal lobe areas changes as monkeys learn new associations[27–32].

Decisions with uncertain alternatives. Many psychophysics experiments require subjects to choose between stimuli that are difficult to discriminate. For
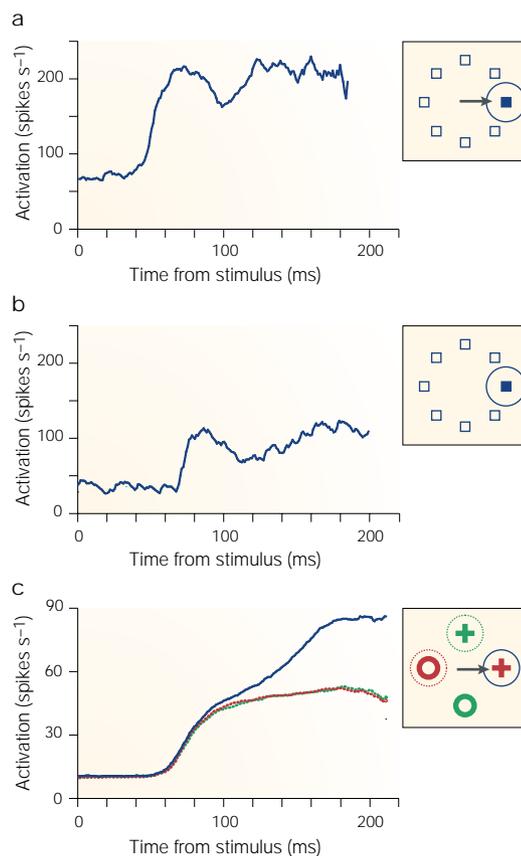
Figure 2 | **Neural correlates of a choice in visual search.**
a | The activity of a neuron in the frontal cortex of a monkey shifting gaze to the single conspicuous stimulus. The response to the target (dark-blue solid line), and the response to the distractor (light-blue dotted line) are superimposed for comparison. The inset portrays the stimulus array with superimposed receptive fields symbolizing the corresponding activation. After about 100 ms, a selection process transpires that results in an explicit representation of the location of the target. **b** | Response of a single neuron in frontal cortex to the conspicuous oddball (dark-blue solid line) and to the distractor (light-blue dotted line) when the array was presented but no gaze shift was made. Fixation maintained at the centre is indicated by the dotted circle. **c** | Average responses of many neurons in frontal cortex to the different stimuli in an array that requires a search for a conjunction of colour and shape. The activation (dark-blue solid line) was greatest for the red-cross target. The response to the distractors varied according to the visual similarity of the distractor to the target (red, green and blue dotted lines). (Figure modified with permission from REF. 19 © (1996) and REF. 21 © (1997) American Physiological Society; and from REF. 23 © (1999) Macmillan Magazines Ltd.).

BACKWARD MASKING
The reduced perception that occurs when a weak stimulus is followed immediately by a stronger stimulus.

BINOCULAR RIVALRY
The perceptual alternation that occurs when markedly different stimuli are presented to the two eyes – for example, horizontal bars in one eye and vertical bars in the other.

choices and the activity of individual neurons in the middle temporal (MT) visual area; moreover, although weak, the relationship is clear even when the motion signal is weak or absent[34]. These observations indicate that this perceptual decision can be based on the weakly correlated activity of a small population of area MT neurons, combined with some additional noise to signal the alternative directions of motion[35]. Comparable observations have been made in somatosensory cortex of monkeys performing a tactile judgement[36,37].

This research has shown that neural activity in sensory areas manifests the evidence on which the decision is based. How do centres in the brain that produce the behavioural response make use of the signals in sensory cortex? Several recent studies have focused on the neural processes in the superior colliculus, the lateral intraparietal area and the frontal eye field, because these gaze-control structures have a more direct role in producing the eye movement with which monkeys report the direction of motion in the random dot display[38–40]. Neurons in each structure produced activity that predicted the choice between the two alternatives that the monkeys eventually made (FIG. 3c). Although the activity of neurons in area MT only subtly distinguished between the alternatives when there was no net motion or when the monkeys made errors[34], the activity of neurons in the gaze-control structures evolved to signal the choice that the monkey made and not the evidence upon which that choice was made. Thus, neurons in the gaze-control structures signal something beyond the sensory evidence. Comparable findings have been made in the frontal eye field in an experiment that used BACKWARD MASKING to create a condition in which the same physical stimulus might or might not be detected and localized[41,42] and in primary motor cortex and premotor cortex of monkeys performing a tactile discrimination task[43,44].

In these studies of the neural processes associated with decision making, investigators could predict which choice would be made by monitoring the activity of particular neurons. In some experiments this was possible during individual trials. For example, in a study of monkeys reporting their percept during BINOCULAR RIVALRY[45], the activation of particular neurons during presentation of the ambiguous stimulus was a very reliable predictor of what choice monkeys would make a second later.

Manipulating and probing decisions
If prediction is one side of understanding, the other side is manipulation. Recent studies have used electrical stimulation of cortical sensory areas to probe how brain activity relates to the process of deciding. For example, electrical stimulation at different frequencies in somatosensory cortex of monkeys cannot be distinguished from a natural fluttering stimulus on the finger[46]. In monkeys trained to discriminate the direction of motion of a visual stimulus, electrical stimulation of area MT increases the probability that the monkey will choose the preferred direction represented at the stimulated site[47,48]. The stimulation is effective when applied during presentation of the visual motion display but is less effective when applied before or after the display[49].

example, monkeys have been trained to report the net direction of motion in a field of randomly moving dots. In these experiments the proportion of dots that move in the same direction is varied by the experimenter to manipulate the ambiguity between the alternatives[33] (FIG. 3). As the fraction of dots moving in random directions increases (diluting the motion signal) the proportion of correct responses decreases. Now, for a given stimulus the behavioural response can vary; likewise, the response of a neuron to a given stimulus can vary. Nevertheless, a relationship has been observed between the behavioural

Thus, electrical stimulation of area MT influences visual processing rather than the decision process directly.

Electrical stimulation can be used not only to manipulate but also to probe transpiring decisions. Stimulation of the frontal eye field has been used to probe the formation of the decision in the motion discrimination task[50]. As before, monkeys signalled their decision about the direction of motion by producing an eye movement in either of two directions. In a random fraction of trials, electrical stimulation was applied to the frontal eye field to elicit an eye movement. The stimuli were arranged so that the saccade evoked by electrical stimulation was perpendicular to the choice saccades. The investigators found that the direction of the saccade evoked by the electrical stimulation was influenced by the direction of the eye movement that the monkeys were to make to signal the direction of motion. In other words, if the monkey was going to produce an upward saccade to signal upward motion, then the horizontal saccade evoked by the electrical stimulation deviated slightly upward.

The magnitude of the deviation was proportional to the strength of the motion signal and the duration of the motion presentation. The investigators showed that the deviation can be explained in terms of a hypothetical accumulating signal that corresponds to the extent of discrimination of the direction of motion by the population of neurons in area MT. One accumulator that represents the motion in the direction of the correct choice grows in proportion to the strength of the signal. Another accumulator that represents motion in the direction of the incorrect choice grows more slowly. The deviation of the evoked eye movement is proportional to the difference between the accumulated correct and accumulated incorrect values in this model.

These data show that what monkeys sense and do can be influenced by artificially activating discrete parts of the brain. This evidence indicates that brain circuits underlying more complex perceptual and cognitive processes, once they are located and characterized, might be activated artificially to influence more complex decisions.

Choices and reasons

When we say that choosing is selecting one among a set of alternatives for some purpose, we exclude cases in which it makes no difference what the alternatives are. If each of the meals in the restaurant were equally unknown or satisfying, then whatever you select would not be a real choice. According to this view, to say that one expresses a choice implies that there is a connection between which action one performs and some preference or desire. To explain this connection is to give a reason for why one alternative was chosen. How reasons and desires came to be and relate to producing actions are still matters of discussion[51–53]. An account of 'how' the choice was made in terms of brain events such as those described so far does not seem to capture the reason 'why' the choice was made. If we wish to have a complete account of choosing and deciding in terms of brain processes, then we must also explain the neural basis of reasons for choices. Such an account
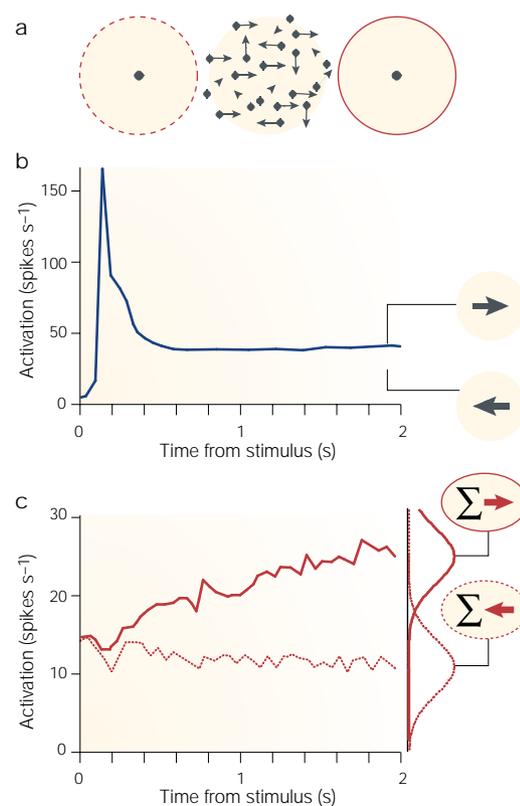

Figure 3 | **Neural correlates of a perceptual decision.**
a | Monkeys viewed a field of dots moving in random directions with a variable fraction moving in one of two directions, in this case rightward. To dissociate the representation of the stimulus from the formation of the decision, the signal to generate the behavioural report was given 2,000 ms after the motion stimulus was presented. Monkeys reported the net direction of motion by shifting their gaze to one of two spots that appeared on either side, after the field of dots was removed. The receptive fields of four neurons are portrayed, two covering the random dots (light-blue dotted and dark-blue solid lines), preferring opposite directions, and one covering each response spot (red solid line and red dotted line). b | The visual representation of the alternative directions of motion in a display with only 25% of the dots moving in the same direction for a unit that responds preferentially to rightward motion (dark-blue solid line) and for a unit that responds preferentially to leftward motion (light-blue dotted line). The receptive fields of both neurons cover the motion display as indicated in a. After an initial transient response, the maintained activity remains at a constant level corresponding to more (dark-blue solid line) or less (light-blue dotted line) strength of the motion in the preferred direction. The data were drawn from a single neuron. (Panel b modified with permission from REF. 126 © (1993) Cambridge University Press.) c | Neural representation of the perceptual decision as an accumulating sum of the strength of the motion in the alternative directions. The activation of neurons at this stage of processing is preliminary to orientating to one of the target spots as indicated by the response fields drawn in red in a. Owing to variability in neuronal responses in the visual representation, the magnitude of the accumulated evidence forms distributions of high (red solid line) and low (red dotted line) values. The choice of which eye movement to produce is dictated by the larger of the alternative accumulated values. Because of random variability in the values that are accumulated in different trials, it can happen that a monkey will report leftward motion even though net rightward motion is present. (Panel c modified with permission from REF. 38 © (1996) National Academy of Sciences, USA.).

might be possible if we could determine the neural basis of preferences and desires.

In economics and psychology, the reason for a choice is referred to as utility[1,54]. Choices relate to utility in certain lawful ways[55]; choices among alternatives are guided by the utility that they provide among payoffs varying in magnitude, probability and kind. Positive utilities (rewards) are approached; negative utilities (punishments) are avoided. The utility of a given set of

a | Basic actions are produced when the activity of movement neurons reaches a fixed threshold. Variability in the time of initiation of the action originates in the variable time taken for the activity to grow to the threshold. The thickness of the line is proportional to the probability of occurrence. Insets show the sequence of visual events. (Panel **a** modified with permission from REF. 9, taken from the *Annual Review of Neuroscience*, Volume 22 © (1999) by Annual Reviews www.AnnualReviews.org.) **b** | Exerting control through cancelling a planned movement. Plots compare the activity of a gaze-shifting neuron (top) and a gaze-holding neuron (bottom) in trials in which the movement was produced, but would have been cancelled if the stop signal had been presented (blue line) with the activity in trials when the planned movement was cancelled because the stop signal (red square at fixation) appeared (red line). The onset of the stop signal is indicated by the solid vertical arrow. The time needed to cancel the planned movement is indicated by the tinted area. The rapid change in activation of both types of neuron immediately before the movement cancellation time shows that the activation of these neurons is sufficient to control whether an action will occur. (Panel **b** modified with permission from REF. 91 © (1998) American Physiological Society.)

Figure 4 | **Neural control of a purposeful eye movement.**

alternatives depends not only on their respective properties but also on the state of the chooser. Your choice of a meal in the restaurant will vary according to your last meal — what it was and when it occurred.

A key insight into the brain mechanisms of utility was the discovery that animals and humans will work to obtain electrical stimulation delivered to certain parts of the brain[56]. Brain-stimulation reward shares many properties with natural rewards; unfortunately, the extensive literature in this area is beyond the scope of this article[57–59]. Several studies have documented the influence and representation of reinforcement in the brain. Neural activity in sensorimotor as well as limbic structures is modulated by the probability, magnitude or kind of reward that a monkey receives[60–64], and such modulation can guide adjustments in behaviour[65]. Neural activity more explicitly signalling the receipt, withholding or unexpected delivery of reward has been found in several brain structures[66]. For example, neurons in orbital frontal cortex are active in anticipation of rewards, and the level of activity corresponds to the preference for the particular reward relative to others available[67]. Such neural activity has figured in models of how reinforcements guide behaviour[68–74]. This body of empirical and theoretical work seems to form a foundation for describing the neural basis of reasons for choices.

Neural correlates of acting

Once desire, opportunity and ability are aligned and a decision has been made, the appropriate action must be executed. Curiously, the precise time of initiation of an action is unpredictable. This unpredictability is captured in measurements of RESPONSE TIMES, and these range from as low as 100 ms to more than 1,000 ms. The duration and variability of response times have been a central problem in psychology because they cannot be explained simply by transduction and neural transmission delays[75–78].

Recent neurophysiological studies have indicated how the brain prepares and initiates movements. Note that the results to be described were obtained from neurons that are qualitatively different from the type of sensory neuron we have considered so far. Eye movements are controlled by the balance of activity in two classes of neurons in gaze-control structures such as the frontal eye fields or superior colliculus. The first are 'movement' neurons because gaze shifts occur when they are activated[79,80]. The second are 'fixation' neurons because gaze shifts are prevented when they are activated[81,82]. Both kinds of neuron exert a direct influence on brainstem eye-movement nuclei.

Eye movements are produced when movement-related neuron activity increases and fixation neuron activity decreases by a sufficient amount. A movement is initiated when the movement-related neural activity reaches a particular threshold[83–86] (FIG. 4a). The threshold does not vary with response time, so the variability in response time arises because the time taken for the movement-related activity to grow to the threshold is random. This sign of movement preparation is observed in single neurons, and it parallels electrical potentials recorded from
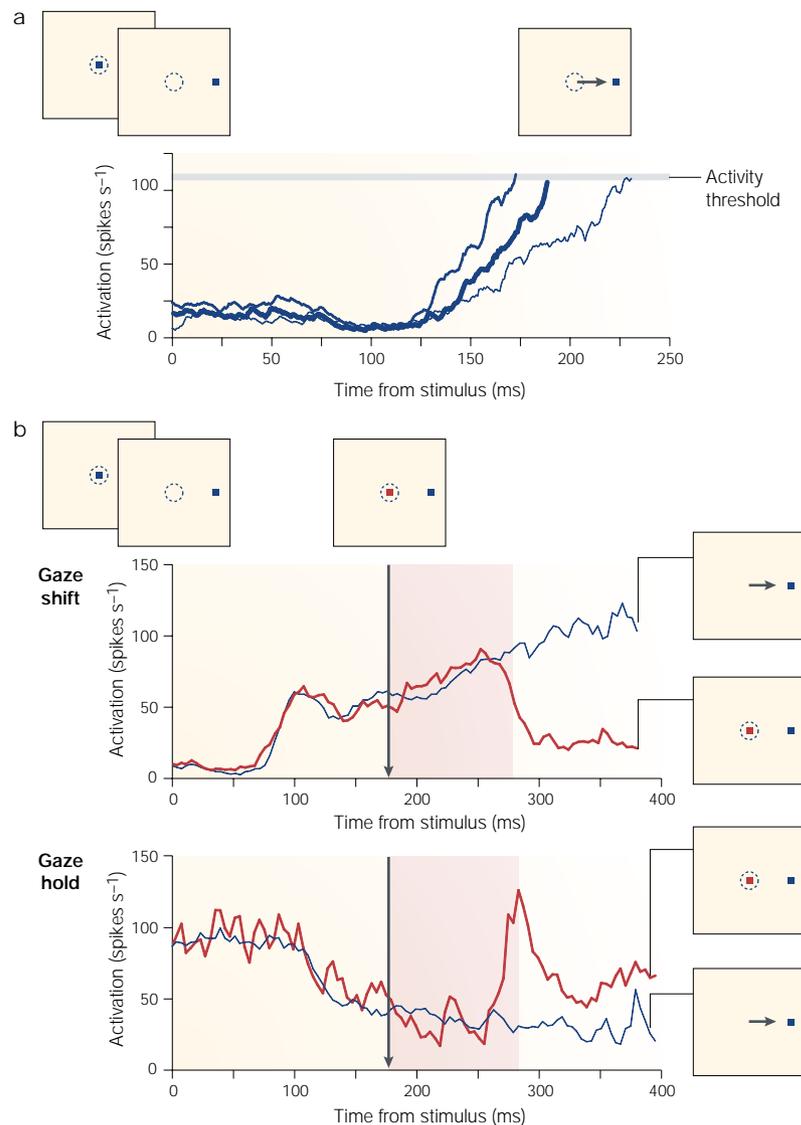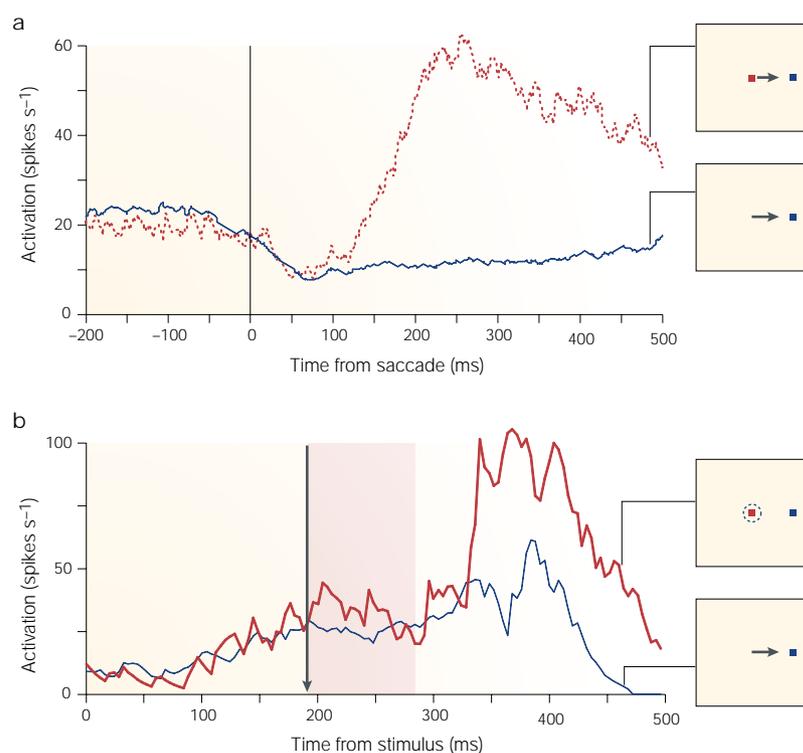
Figure 5 | **Neural correlates of performance monitoring. a** | Comparison of activity between trials when the movement was made because no stop signal was given (blue solid line) and trials when the movement was made in spite of the stop signal (red dotted line). The activation signals the occurrence of an error. **b** | Comparison of activity between trials when the movement was cancelled (red solid line) and trials when the movement was produced but would have been cancelled if the stop signal had been presented (blue solid line). The onset of the stop signal and the estimated time to movement cancellation are indicated as in **FIG. 4**. The activation after the movement was cancelled might signal that the mutually incompatible processes of shifting and holding gaze were activated simultaneously. (Modified with permission from **REF. 101** © (2000) Macmillan Magazines Ltd.)

RESPONSE TIME
The time that elapses between presentation of a stimulus requiring a behavioural response and the time of initiation of the response.

RACE MODEL
A common model in cognitive psychology in which a behaviour is supposed to be the outcome of a race between two or more processes that have random finish times. Race models have been used to explain choice behaviour and the control of actions.

the scalp before movements[87] and closely resembles the architecture of certain models of reaction time[88–90].

Commonly, brain structures are attributed a function in motor control if they can be shown to have a role in producing movements; however, self-control is commonly expressed by withholding actions. A recent experiment has described how planned actions are cancelled[91]. The ability of subjects to control the initiation of movements was investigated in a reaction-time task in which an imperative stop signal that called for subjects to cancel the planned response was presented on an infrequent basis. Performance in this countermanding task can be simulated with a simple race between two processes: one that produces movements and another that inhibits movements[92–94]. This RACE MODEL provides a means of estimating the time needed to cancel a planned movement.

Signals produced by single neurons that are sufficient to control the production of movements have been identified in the frontal eye field of monkeys performing this task[91]. When planned movements were cancelled, movement-related activity, after beginning to grow towards the trigger threshold, decreased rapidly after the stop signal was presented (FIG. 4b). Moreover,

the reduction of movement-related activity that occurred when the movement was cancelled happened just before the time that the movement was cancelled, as estimated by the race model. Conversely, fixation neurons, which normally show decreased activity with eye movements, exhibited a rapid increase in firing when movements were cancelled. Therefore, the activity of single neurons in motor structures is sufficient to specify whether or not a movement will be produced. Complementary results have been obtained with scalp potentials[95,96].

These findings show that movements can be prepared but not executed. Execution happens only if the preparation occupies sufficient time to allow an organism to react to unexpected changes in the environment. The ability to cancel evolving motor plans confers flexibility and adaptability on behaviour. But what if errors are made? Organisms must recognize errors and adapt their behaviour to minimize future mistakes. Some brain system must therefore monitor the consequences of action to adjust performance.

Neural correlates of evaluating consequences

The esteemed ability to make good choices is too often gained through the hard experience of making bad choices. Recent functional imaging and event-related potential studies, and single-neuron recordings in monkeys, have provided new information about how the brain monitors behaviour. This work contributes to our understanding of the executive processes that monitor and control the perception, selection and production systems[97–100].

In monkeys performing the countermanding task, certain neurons in the supplementary eye field are modulated specifically in trials in which a planned movement is not cancelled as it should be[101] (FIG. 5a). This signal appears to register the occurrence of an error and seems to correspond to a scalp potential called the error-related negativity, which is recorded in humans when errors are produced in a variety of conditions[102–106]. Errors are commonly produced in situations that call for a choice between incompatible actions within a deadline. An alternative interpretation of the brain activation associated with errors is that it measures the conflict arising when two or more mutually incompatible cognitive processes are engaged[107]. Functional brain imaging studies have produced evidence consistent with this hypothesis[108–111]. Neural activity recorded in the supplementary eye field can also be viewed in this light. Some neurons discharge more during trials in which the movement is correctly cancelled, but the activity occurs after the movement is cancelled[101] (FIG. 5b). This modulation clearly does not signal an error, and it cannot be involved in cancelling the movement because it occurs too late. In trials with successfully cancelled eye movements, both gaze-shifting movement neurons and gaze-holding fixation neurons were activated concurrently[91] (FIG. 4). In fact, the magnitude of this modulation in trials with successfully cancelled movements increases with the amount of combined activation of gaze-shifting and gaze-holding neurons. This relation-

ship is consistent with the hypothesis that these neurons are signalling the conflict arising from co-activation of mutually incompatible processes. A third class of neuron in the supplementary eye field signals the anticipation and receipt of reinforcement[101,112].

Neural representations of error, conflict and reinforcement form important constituents of a supervisory executive system. How signals like these influence sensory and motor brain centres is not clear yet. The characterization of neural correlates of executive processes is an active area of research, and further insights should be forthcoming.

Implications

The realization that decisions originate in deterministic brain processes follows from the rejection of dualism. The neurophysiological studies that we have reviewed show that the neural correlates of deciding, choosing, acting and evaluating are not too complex to identify or even manipulate. At least in certain experimental domains, an agent's choice appears to hinge on the activation of a surprisingly small number of neurons in discrete parts of the brain. Thus, by monitoring the signals produced by appropriate neurons, an experimenter can predict and even influence what monkeys will choose, even though we do not yet know how these signals are produced by the circuits of the brain. Ethics, not theory, would preclude an investigator from obtaining the same relationship with the brain of a human agent[113]. Can this ability to predict and influence choices be reconciled with a belief in freedom and responsibility[114]?

The ability to predict and influence choices provides compelling evidence that choices are deterministic. Certainly, to the extent that neurons will not discharge unless they are depolarized by other neurons, brain states can be determined naturally only by earlier brain states. However, does such apparently Laplacian determinism grant as much prediction and influence as the evidence seems to indicate? Perhaps not. Complex dynamic systems that are far from equilibrium are usually not predictable[115]. The brain is without doubt such a dynamical system[116,117] that produces behaviour with the signature of chaos[118,119]. In fact, some have argued that cognition is at least as dynamical as it is computational[120–122]. Thus, the states of the brain, like the clouds in the sky, happen because of earlier states of the system.

But brain states and behaviour can be as unpredictable as the weather. If current research is correct — that choices derive from states of the brain, and states of the brain, although deterministic, are not entirely predictable — then it follows that choices may be made that are unexpected. Certainly the world is an unpredictable place, and it seems almost self-evident that the behaviour of most creatures, including humans, can be unpredictable[123,124]. As we survey this landscape, we should realize that all of the neurophysiological results that we have reviewed were obtained after weeks of training monkeys to perform rigidly constrained tasks in impoverished environments, quite unlike the real world[125]. Accordingly, conclusions drawn from the results of these experiments should be generalized to real-world situations with caution.

Still, the results that I have reviewed seem relevant to understanding freedom of choice. If we ask whether we are free, the kind of answer we want may not be possible[6]. A better question to ask is: do we make choices? The answer is certainly yes. Do our choices have any influence on our relationship to our peers and the environment? Again, yes. Are our choices constrained? Yes, because of natural law and historical circumstances, but not entirely because of random chance and deterministic chaos[6]. Consider a game of cards. To begin a fair game, the cards are shuffled to introduce randomness that produces unpredictability and lack of control over what cards are drawn. Once the hands are dealt, your freedom to play a certain card is limited by the rules of the game, the hand you are dealt, and your knowledge of strategy and tactics. But within these limitations you have many choices to react to, or anticipate what other players do — both the astute tactics and the blockheaded blunders. The moment of deliberation about which card to play seems to embody all of the freedom one could hope for. The fact that such deliberation is accomplished by your brain takes away none of the joy of the game.

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FURTHER INFORMATION Schall lab homepage

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