

A general mechanism for decision-making in the human brain?

Alan E. Rorie and William T. Newsome

Howard Hughes Medical Institute and Department of Neurobiology, Stanford University School of Medicine, Stanford, CA 94305, USA

A new fMRI study by Heekeren and colleagues suggests that left dorsolateral prefrontal cortex (DLPFC) contains a region that integrates sensory evidence supporting perceptual decisions. DLPFC meets two criteria posited by Heekeren *et al.* for such a region: (1) its activity is correlated in time with the output of sensory areas of the visual cortex measured simultaneously, and (2) as expected of an integrator, its activity is greater on trials for which the sensory evidence is substantial than on trials for which the sensory evidence is weak. Complementary experiments in humans and monkeys now offer a realistic hope of elucidating decision-making networks in the primate brain.

Jurors often make difficult decisions of utmost importance to society. Importantly, we do not allow jurors to accomplish their task by any means whatsoever; they cannot, for example, decide by flipping coins, rolling dice or drawing straws. Ideally, jurors attend carefully and equally to all sources of evidence, progressively integrating the evidence until they can make a well informed judgment of guilt or innocence. A growing body of research suggests that the brain makes decisions in a similar

manner – integrating various sources of evidence until an informed judgment can be made.

A recent experiment by Heekeren and colleagues [1] provides new evidence supporting an integration model of decision-making in human subjects. Functional MRI data obtained while subjects categorized visual images suggest that dorsolateral prefrontal cortex (DLPFC) integrates the neural evidence used to make perceptual decisions. This experiment was motivated and informed by the work of Shadlen and Newsome who first presented neurophysiological evidence for the integration model by recording from single parietal lobe neurons while rhesus monkeys performed a visual direction discrimination task [2] (Box 1).

fMRI evidence for an ‘integration’ area

The Heekeren study was designed to be roughly analogous to the Shadlen and Newsome experiments. The researchers asked their human subjects to categorize images as either houses or faces. The images were clear on half of the trials, but were masked by noise on the remaining half (Figure 1). The clear images therefore provided strong evidence for the decision and the noisy images provided

Box 1. Neurophysiological evidence for the integration model

In the Shadlen and Newsome experiments [2] a monkey viewed a field of random dots in which a specified proportion of the dots moved coherently in one direction and the remaining dots masked the coherent motion signal with random motion noise. The monkey’s job was to determine on each trial whether the coherent motion signal moved in one direction or its opposite (e.g. right versus left). The proportion of dots in coherent motion varied from trial-to-trial, with the result that motion direction was exceedingly difficult to discriminate on some trials (low proportions of coherent dots) but was easy on other trials (high proportions of coherent dots).

Previous studies had shown that motion-sensitive neurons in the middle temporal visual area (MT) provide sensory signals that are used by the monkey to judge the direction of motion [3,4]. Shadlen and Newsome posited that the monkey’s perceptual decisions are based on the difference in activity between one pool of MT neurons that responds best to rightward motion and a second pool that responds best to leftward motion [2,5]. The output of the two MT pools provides an instantaneous measure of the fluctuating motion ‘energy’ in the random dot stimulus as function of time, one for rightward motion and one for leftward. After separately integrating (in the mathematical sense) the output of these two pools of MT neurons over time – two seconds in the original experiments – one can calculate a

‘decision variable’ by subtracting one integrated output from the other (right versus left). The decision is cast in favor of the direction accruing the most evidence.

Shadlen and Newsome showed that neurons in the lateral intraparietal area (LIP) of the parietal lobe seem to perform this integration function [2,5]. One pool of LIP neurons, corresponding to the actual direction of coherent motion, exhibited gradually increasing activity as although it were integrating the positive output of the corresponding pool of MT neurons. As expected, the rate of increase correlated well with the coherence of the motion stimulus. A second pool of LIP neurons appeared to integrate the output of MT neurons responding to the opposite direction of motion. (Neurons with similar properties were later observed in the frontal lobe and in a midbrain structure as well [6–8].) Shadlen and colleagues subsequently showed that the integrator model accounts for observed variation in both the accuracy of the monkey’s decisions and in the time taken to make the decision (reaction time) as a function of the coherence of the motion signal [9,10]. Although Shadlen and Newsome proposed this as a general model for decision-making, the model has not been tested neurophysiologically outside the realm of visual discrimination in rhesus monkeys.

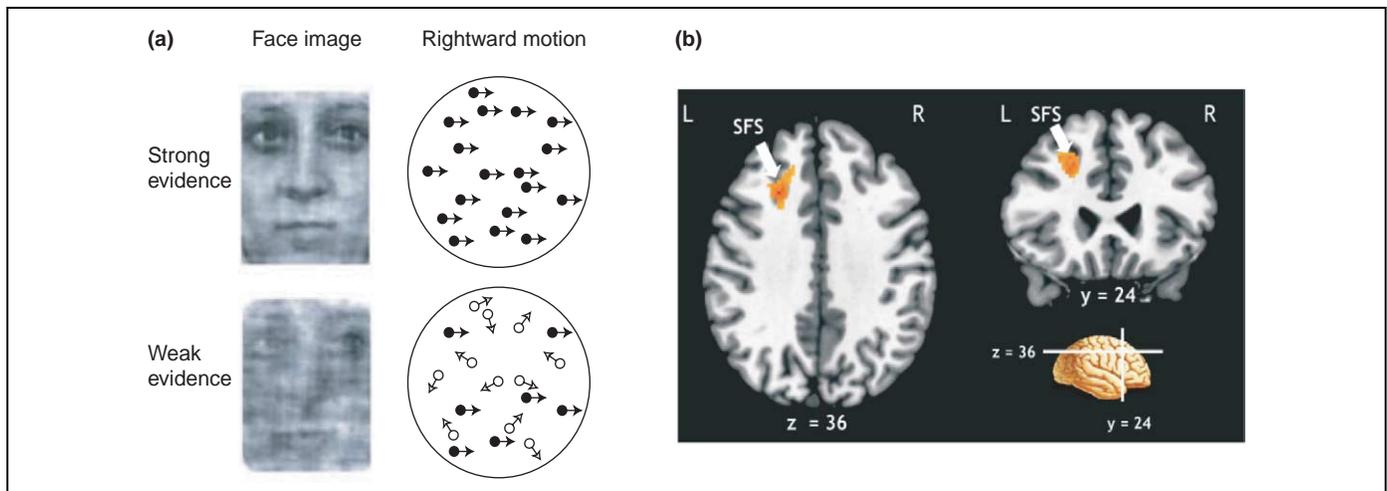


Figure 1. Decision-making in the human brain. (a) Left: visual stimuli used in the study of human decision-making by Heekeren *et al.* The upper face image is clear, only mildly degraded by noise. The lower image of the same face is degraded by noise, rendering it somewhat difficult to identify as a face. Right: visual stimuli used in the study of decision-making in monkeys by Shadlen and Newsome [2]. The upper frame depicts a stimulus composed of dots moving coherently to the right. The rightward motion signal is undegraded by noise and easily discriminated from leftward motion. By contrast, in the lower frame the rightward motion is degraded by random motion noise, rendering the stimulus more difficult to discriminate from leftward motion. (b) Location of left dorsolateral prefrontal cortex (DLPFC) in the superior frontal sulcus (SFS), the region of the human brain that met both predictions for an area that integrates sensory evidence needed to support a perceptual decision. (Reproduced with permission from [1]).

weak evidence. Predictably, subjects made more correct categorizations with stronger evidence.

Using houses and faces as the stimuli, rather than motion, was an insightful approach. This choice enabled Heekeren *et al.* to exploit the (somewhat curious) finding that faces and houses selectively activate separate sensory regions of human ventral temporal cortex [11]. Importantly, the researchers demonstrated that the magnitude of activation of each of these areas is proportional to the clarity of the image: the ‘face’ area responded increasingly better as noise was progressively removed from images of faces and worse as noise was removed from the images of houses. The ‘house’ area exhibited the converse pattern of responses. On each trial, therefore, the researchers subtracted the responses of the two areas to assess the strength of the neural evidence supporting the discrimination. Note that this approach would have been impossible using motion (as Shadlen and Newsome did) because the spatial resolution of fMRI is insufficient to image pools of MT neurons representing single motion directions. Armed with this neural ‘read-out’ of the sensory evidence, the researchers set out to identify brain areas that might integrate such evidence to form perceptual decisions.

Heekeren and colleagues argue that any area integrating the neural evidence supporting the decision should meet two requirements. First, like the single neurons studied by Shadlen and Newsome, an area that integrates sensory evidence should be most active when the evidence is greatest and the decision easy. Second, the magnitude of the integrated activity should correlate on a trial-to-trial basis with the strength of the sensory evidence passed on from the visual system; that is, the time series of decision-related activations measured across trials should be correlated with the time series of *activation differences* from the house and face areas of ventral temporal cortex measured on the same trials. Remarkably, only one area of the human brain satisfied both requirements: the left dorsolateral prefrontal cortex

(DLPFC). Heekeren and colleagues propose that this area of the human brain may contain a general mechanism for integrating perceptual evidence for decision-making.

A particularly pleasing aspect of this study is that the experimental design contains a nice control for the effects of attention. Whereas an ‘integrator’ area should be more active on easy trials (lots of sensory evidence available), brain areas involved in attention should be more active on difficult trials. Indeed, the researchers found that a well known constellation of attention-related areas is more active on difficult trials, including the frontal eye fields (FEF) [12,13] and the intraparietal sulcus (IPS) [14].

Is the neural decision-making circuitry the same in monkeys and humans?

Although the Heekeren *et al.* study provides interesting new evidence for a perceptual decision-making module in left DLPFC, many interesting questions remain to be answered. Foremost among them, perhaps, is why only a single area of the human brain conformed to the integrator hypothesis, whereas neurons with integrator functions were observed in single-unit studies of several areas of the monkey brain, including prefrontal cortex [6], LIP [4,5] and the superior colliculus [7,8].

One possible answer to this question is that because of its poor spatial resolution, fMRI only detects signals in areas with physiologically homogeneous populations, whereas single-unit studies can detect signals in physiologically heterogeneous populations. In this model, the integration process is detected in human DLPFC because neurons performing this function constitute a majority of the population. Such neurons may be present in other, more heterogeneous areas, but fMRI is simply blind to them. However, such a model requires reconciliation with experiments on other decision tasks suggesting that a relatively homogeneous population of neurons populates the DLPFC [15].

A second, more interesting possibility is that the organization of decision-making circuitry is fundamentally different in monkeys and humans. In the studies from the Shadlen and Newsome laboratories, the monkeys indicated their perceptual decisions by making eye movements to visual targets, and decision-related signals were observed correspondingly in brain regions linked in previous studies to preparation for eye movements. Human subjects in the Heekeren *et al.* study indicated decisions by means of a button press. By analogy, one might have expected to detect decision-related signals in premotor areas of the cortex linked to hand movements – areas that were conspicuously absent from the list of responsive areas in the study. Perhaps humans have evolved a more abstract decision-making module that is functionally separate from the motor effector systems that prepare and execute responses. For monkeys it may be the case that to see and decide is, in effect, to plan a motor response. For humans, on the other hand, the link between decision and action may well be more flexible, permitting longer lead times and more sophisticated processing between decision and action.

Conclusion

The Heekeren *et al.* study will no doubt be followed up in various ways. But to our minds, one of the most important experiments would be to image the brains of monkeys performing a task that is as identical as possible to the one performed by the human subjects in the current study. Only by doing this will we be able to determine whether the global pattern of activation in the monkey brain is similar to or substantially different from that in the human brain during decision-making. If the two patterns are similar, the monkey imaging study could identify the precise cortical area that corresponds to DLPFC in humans, thereby enabling physiologists to target it for detailed electrophysiological study. Plainly, our suggestion incorporates a vision of the future in which monkey and human experiments, and imaging and electrophysiological experiments, are carried

out in tandem to explore more incisively the higher functions of the primate brain.

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Book Review

If bears eat in the woods...?

If by Jonathan St B.T. Evans and David E. Over, Oxford University Press, 2004. £27.95 (pbk) (vii + 190 pp.) ISBN 0198525133

Philip N. Johnson-Laird

Stuart Professor of Psychology, Department of Psychology, Princeton University, Green Hall, Princeton NJ 08544, USA



'If' is the most problematical two-letter word in the language. And conditional assertions, which it forms, have been a headache for analysts for over 2000 years. Children know what the word means, and so do you – until I ask you to tell me. Jonathan Evans, a psychologist, and David Over, a philosopher, are a

long-standing team of experts on reasoning, and they have joined forces again to try to crack this puzzle. Following Edgington [1], they distinguish three sorts of theory about the meaning of 'if', and they try to decide which of them is best.

Consider the conditional:

If Bacon wrote Hamlet then Shakespeare didn't

and ask yourself in what circumstances it would be true.

Corresponding author: Johnson-Laird, P.N. (phil@princeton.edu).