a ternary subcomplex of Borealin, Survivin, and the N-terminal domain of INCENP. Mol. Biol. Cell *17*, 2547–2558.
4. Lens, S.M., Rodriguez, J.A., Vader, G., Span, S.W., Giaccone, G., and Medema, R.H. (2006). Uncoupling the central spindle-associated function of the chromosomal passenger complex from its role at centromeres. Mol. Biol. Cell *17*, 1897–1909.
5. Gassmann, R., Carvalho, A., Henzing, A.J., Ruchaud, S., Hudson, D.F., Honda, R., Nigg, E.A., Gerloff, D.L., and Earnshaw, W.C. (2004). Borealin: a novel chromosomal passenger required for stability of the bipolar mitotic spindle. J. Cell Biol. *166*, 179–191.
6. Jeyaprakash, A.A., Klein, U.R., Lindner, D., Ebert, J., Nigg, E.A., and Conti, E. (2007). Structure of a Survivin-Borealin-INCENP core complex reveals how chromosomal passengers travel together. Cell *131*, 271–285.
7. Wang, F., Dai, J., Daum, J.R., Niedzialkowska, E., Banerjee, B., Stukenberg, P.T., Gorbsky, G.J., and Higgins, J.M. (2010). Histone H3 Thr-3 phosphorylation by Haspin positions Aurora B at centromeres in mitosis. Science *330*, 231–235.
8. Kelly, A.E., Ghenoiu, C., Xue, J.Z., Zierhut, C., Kimura, H., and Funabiki, H. (2010). Survivin reads phosphorylated histone H3 threonine 3 to activate the mitotic kinase Aurora B. Science *330*, 235–239.
9. Dai, J., Sultan, S., Taylor, S.S., and Higgins, J.M. (2005). The kinase haspin is required for mitotic histone H3 Thr 3 phosphorylation and normal metaphase chromosome alignment. Genes Dev. *19*, 472–488.
10. Dai, J., Sullivan, B.A., and Higgins, J.M. (2006). Regulation of mitotic chromosome cohesion by Haspin and Aurora B. Dev. Cell *11*, 741–750.
11. Tsukahara, T., Tanno, Y., and Watanabe, Y. (2010). Phosphorylation of the CPC by Cdk1 promotes chromosome bi-orientation. Nature *467*, 719–723.
12. Kawashima, S.A., Tsukahara, T., Langegger, M., Hauf, S., Kitajima, T.S., and Watanabe, Y. (2007). Shugoshin enables tension-generating attachment of kinetochores by loading Aurora to centromeres. Genes Dev. *21*, 420–435.
13. Vanoosthuyse, V., Prykhozhij, S., and Hardwick, K.G. (2007). Shugoshin 2 regulates localization of the chromosomal passenger proteins in fission yeast mitosis. Mol. Biol. Cell *18*, 1657–1669.
14. Sakuno, T., and Watanabe, Y. (2009). Studies of meiosis disclose distinct roles of cohesion in the core centromere and pericentromeric regions. Chromosome Res. *17*, 239–249.
15. Kawashima, S.A., Yamagishi, Y., Honda, T., Ishiguro, K., and Watanabe, Y. (2010). Phosphorylation of H2A by Bub1 prevents chromosomal instability through localizing shugoshin. Science *327*, 172–177.
16. Yamagishi, Y., Sakuno, T., Shimura, M., and Watanabe, Y. (2008). Heterochromatin links to centromeric protection by recruiting shugoshin. Nature *455*, 251–255.
17. Black, B.E., and Bassett, E.A. (2008). The histone variant CENP-A and centromere specification. Curr. Opin. Cell Biol. *20*, 91–100.
18. Huang, H., Feng, J., Famulski, J., Rattner, J.B., Liu, S.T., Kao, G.D., Muschel, R., Chan, G.K., and Yen, T.J. (2007). Tripin/hSgo2 recruits MCAK to the inner centromere to correct defective kinetochore attachments. J. Cell Biol. *177*, 413–424.
19. Resnick, T.D., Satinover, D.L., MacIsaac, F., Stukenberg, P.T., Earnshaw, W.C., Orr-Weaver, T.L., and Carmena, M. (2006). INCENP and Aurora B promote meiotic sister chromatid cohesion through localization of the Shugoshin MEI-S332 in Drosophila. Dev. Cell *11*, 57–68.
20. Hauf, S., Cole, R.W., LaTerra, S., Zimmer, C., Schnapp, G., Walter, R., Heckel, A., van Meel, J., Rieder, C.L., and Peters, J.M. (2003). The small molecule Hesperadin reveals a role for Aurora B in correcting kinetochore-microtubule attachment and in maintaining the spindle assembly checkpoint. J. Cell Biol. *161*, 281–294.

[1]Whitehead Institute for Biomedical Research, Nine Cambridge Center, Cambridge, MA 02142, USA. [2]Department of Medical Oncology, University Medical Center Utrecht, Universiteitsweg 100, 3584 CG, Utrecht, The Netherlands.
E-mail: s.m.a.lens@umcutrecht.nl

DOI: 10.1016/j.cub.2010.09.037

Decision Neuroscience: Choices of Description and of Experience

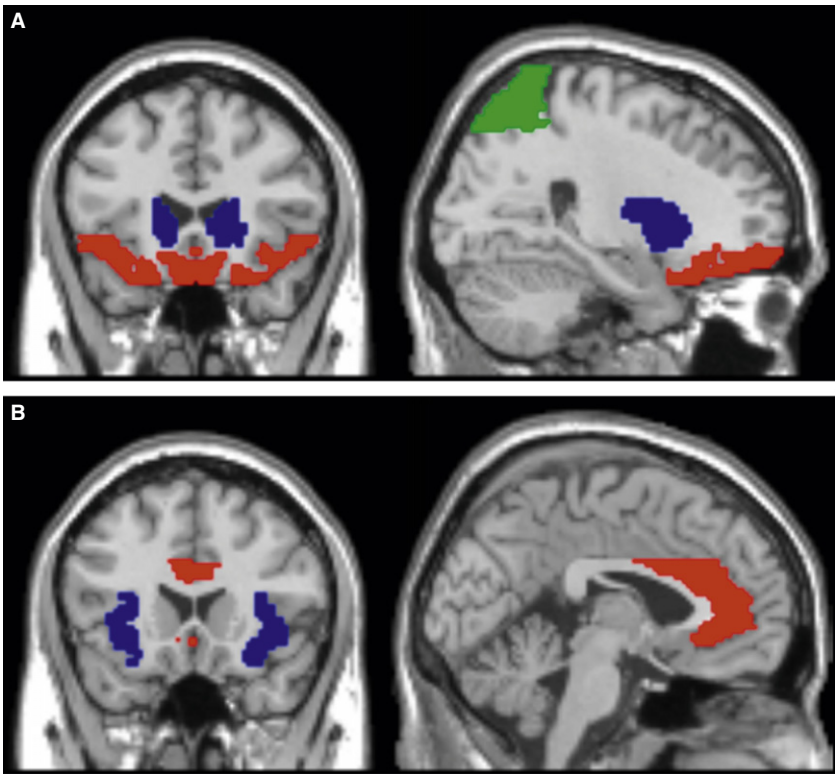
A new study suggests that individuals differentially recruit neural regions associated with decision making, depending on whether the information about the options are learned through experience or merely described.

Ryan K. Jessup and John P. O'Doherty

The ability to make good decisions about future courses of action under conditions of uncertainty is essential for the survival of most animals, including humans. There is a broad consensus among those who study decision making, whether from a theoretical, behavioural or neurobiological perspective, that decisions are typically made through evaluating the expected future benefit (or 'value') that will accrue from choosing each available option and then comparing between those values in order to select the option yielding the largest expected reward [1,2]. When the outcomes of options are uncertain, we must also consider the degree of uncertainty (or 'risk') present [3]. However, recent findings have suggested that the manner in which information is acquired — whether learned or described — fundamentally alters the choice an individual makes [4–6]. A new study reported in this issue of *Current Biology* [7] follows on these behavioural findings, revealing that neural regions are differentially activated depending on whether information about options was acquired through experience versus description.

In studies of the neural basis of decision making, neuroimaging experiments in humans and neurophysiological recordings in other animals are typically concerned with evidence for neural signals related to expected value, and these have revealed a network of brain regions, including (but not limited to) the ventromedial prefrontal cortex (incorporating the medial prefrontal and orbital frontal cortex in the frontal lobes) [8,9], the parietal cortex [10], and the ventral striatum in the basal ganglia [11,12] (Figure 1A). Neural correlates of risk have also been found, particularly in the anterior insular cortex [13,14] as well as in the anterior cingulate cortex [15] (Figure 1B). Decision neuroscientists have elucidated these findings by setting up experimental situations in which their human or animal subjects are presented with choices between varieties of different options. By varying the amount of a reward (such as a monetary gain, or a squirt of juice) available and the probability of obtaining that reward, it has been possible to experimentally manipulate value and risk while simultaneously measuring changes in neural activity.

There are a number of different ways in which the key information about how much reward and what the probability is of obtaining that reward can be conveyed to the experimental subject. One approach, called the 'descriptive method', is to provide an explicit description of the relevant variables associated with each decision option (Figure 2A). For example, a decision trial could be presented as follows: "If you choose option A, there is a 50% probability that you will receive two dollars, otherwise you will receive nothing, whereas if you choose option B, you will receive 1 dollar for certain." A clear advantage of this approach is that it is very easy for an experimenter



Current Biology

Figure 1. Neuroanatomical substrates of decision variables. (A) Regions known to contain valuation signals include the ventromedial prefrontal cortex (colored in red), the striatum (blue) and the parietal cortex (green), shown overlaid on a normalized structural MRI scan at Montreal Neurological Institute (MNI) coordinates: [26, 25, 15]. (B) Regions known to encode risk signals include anterior cingulate (red) and anterior insula (blue) shown at MNI coordinates: [−2, 21, −8].

to vary the magnitude and probability associated with an option by just changing the descriptors used on each trial.

In the alternative 'experiential method', decision variables are not presented explicitly, but instead must be learned by the subject through trial and error (Figure 2B). As before, each option is associated with a unique stimulus or action, but in this case the overt depiction of the option bears no lawful relation to the underlying decision variables associated with that option. Instead, the subject must come to acquire such information through repeated experience of the outcomes available from that option. An advantage of this method is that it is probably a closer approximation of how information about relevant decision variables is acquired in the real world. It is also the dominant approach used to study decision making in animals other than humans (though for a clever example of the descriptive approach in non-human primates, see [9]). A disadvantage of the experiential approach is that it is harder as an experimenter to keep track of the subjects' underlying subjective representation of the relevant decision variables, as these will vary over time and across individuals as a function of differences in experience.

It has become increasingly apparent in the behavioural decision-making literature that these different approaches to the experimental study of decision making differ not only in the nature of information provision, but also in the way in which the acquired information is ultimately used to guide decisions [4–6]. In spite of this burgeoning behavioural evidence, neurobiological studies of decision making to date have failed to address the extent to which differences in presentation might potentially influence the underlying neural representations of those variables.

FitzGerald *et al.* [7] addressed this question head on. These authors used a hybrid decision-making task, in which information about the value and risk associated with some decision options were acquired only experientially, while for other options this information was provided descriptively. They then scanned human subjects by functional magnetic resonance imaging (fMRI) while they made choices between these options, enabling the authors to compare and contrast brain regions involved when encoding decision variables acquired through experience or through description.

Consistent with many previous results, the authors found that activity of the ventromedial prefrontal cortex and the striatum correlated with expected value, while the anterior insula and anterior cingulate cortex was correlated with risk. Intriguingly, however, these areas were found to be differentially engaged under the different presentation conditions: the ventromedial prefrontal cortex was significantly more involved when the value of the chosen option had been acquired through learned experience, whereas the ventral putamen, a part of the ventral striatum, was more engaged when the value of the chosen option had been acquired through description. For risk, the anterior insula was found to be more involved when information had been acquired through description, while the anterior cingulate showed greater correlations with risk when information about the chosen option had been acquired through learning.

These results indicate that decision variables generated on the basis of explicit provision of descriptive information are not processed neurally in the same way as decision variables acquired on the basis of trial and error learning. It is important to note, as acknowledged by the authors [5], that the brain systems identified in the two different conditions are unlikely to be exclusively involved in one or other type of decision making. For instance, the ventromedial prefrontal cortex has previously been found to represent decision values also under conditions involving provision of descriptive information [8,16], while fMRI studies have found activity in the ventral striatum to be correlated with prediction errors, a key signal thought to play a role in trial and error learning, particularly of stimulus-outcome associations [17,18]. A similar story holds true for risk signals in the anterior insula and anterior cingulate [14,15].

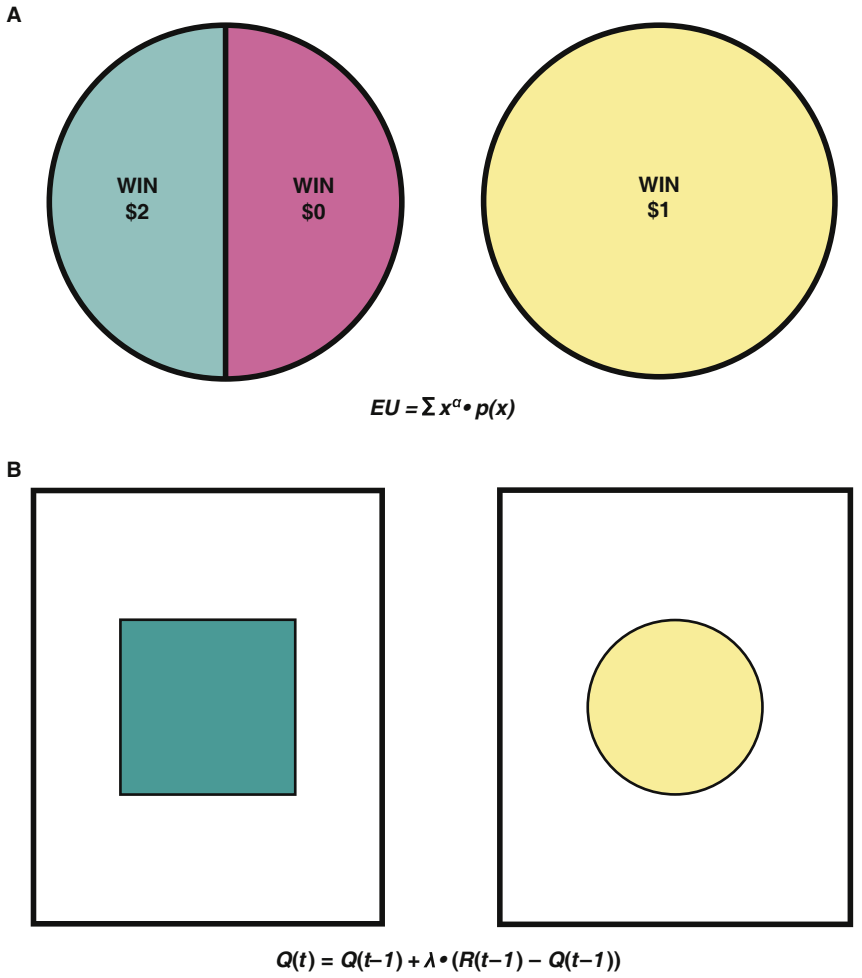


Figure 2. Example option presentation and computation methods.

(A) The descriptive method explicitly states the probability of each possible outcome occurring from each of the two options displayed. Here, the probability of each outcome is conveyed by the area of the circle covered by each color. Expected utility is a typical algorithm used to express descriptive choice and a specific instantiation is shown. The expected utility *EU* for each option is separately calculated by multiplying the utilities of each outcome *x* by the probability *p*(*x*) of the outcome occurring and summing the products. The utility of each outcome is obtained by raising the outcome *x* by the utility parameter α. If $\alpha = 1$, then *EU* is equivalent to the expected value. (B) The experiential method conveys no information about the reward distribution at presentation. Instead, the reward distribution must be learned through repeated play and the reception of outcome feedback. Reinforcement learning is typically used to express experiential choice and a specific instantiation is shown. The learned value *Q* on trial *t* for a particular option is calculated by summing the learned value on the previous trial $Q(t-1)$ with the product of the learning rate parameter λ and the difference of the reward received on the previous trial $R(t-1)$ and $Q(t-1)$, a difference also known as a prediction error.

Rather, the present findings should be interpreted as suggesting that these neural systems may be differentially modulated as a function of the way in which the information is acquired.

More generally, the new findings [5] add to an emerging literature suggesting that the manner in which a decision problem is posed may significantly influence the underlying neural processes recruited to resolve it [19,20]. Even subtle differences in tasks favoured by different research groups could potentially contribute to differences in the underlying engagement of neural systems. An important future direction will be to begin to unravel precisely what factors pertaining to the 'framing' of decision problems contribute to the recruitment of different neural mechanisms, as a stepping stone to understanding how this affects the computations being performed during the decision process.

References

1. Camerer, C.F. (2003). Psychology and economics. Strategizing in the brain. Science *300*, 1673–1675.
2. Glimcher, P.W., and Rustichini, A. (2004). Neuroeconomics: the consilience of brain and decision. Science *306*, 447–452.
3. Preuschoff, K., and Bossaerts, P. (2007). Adding prediction risk to the theory of reward learning. Ann. N. Y. Acad. Sci. *1104*, 135–146.
4. Jessup, R.K., Bishara, A.J., and Busemeyer, J.R. (2008). Feedback produces divergence from prospect theory in descriptive choice. Psychol. Sci. *19*, 1015–1022.
5. Barron, G., and Erev, I. (2003). Small feedback-based decisions and their limited correspondence to description-based decisions. J. Behav. Decision Making *16*, 215–233.
6. Hertwig, R., Barron, G., Weber, E.U., and Erev, I. (2004). Decisions from experience and the effect of rare events in risky choice. Psychol. Sci. *15*, 534–539.
7. FitzGerald, T., Bach, D., Seymour, B., and Dolan, R.J. (2010). Differentiable neural substrates for learned and described value and risk. Curr. Biol. *20*, 1823–1829.
8. Kable, J.W., and Glimcher, P.W. (2007). The neural correlates of subjective value during intertemporal choice. Nat. Neurosci. *10*, 1625–1633.
9. Padoa-Schioppa, C., and Assad, J.A. (2006). Neurons in the orbitofrontal cortex encode economic value. Nature *441*, 223–226.
10. Sugrue, L.P., Corrado, G.S., and Newsome, W.T. (2004). Matching behavior and the representation of value in the parietal cortex. Science *304*, 1782–1787.
11. Knutson, B., Adams, C.M., Fong, G.W., and Hommer, D. (2001). Anticipation of increasing monetary reward selectively recruits nucleus accumbens. J. Neurosci. *21*, RC159.
12. Tobler, P.N., O'Doherty, J.P., Dolan, R.J., and Schultz, W. (2007). Reward value coding distinct from risk attitude-related uncertainty coding in human reward systems. J. Neurophysiol. *97*, 1621–1632.
13. Huettel, S.A., Stowe, C.J., Gordon, E.M., Warner, B.T., and Platt, M.L. (2006). Neural signatures of economic preferences for risk and ambiguity. Neuron *49*, 765–775.
14. Mohr, P.N., Biele, G., and Heekeren, H.R. Neural processing of risk. J. Neurosci. *30*, 6613–6619.
15. Critchley, H.D., Mathias, C.J., and Dolan, R.J. (2001). Neural activity in the human brain relating to uncertainty and arousal during anticipation. Neuron *29*, 537–545.
16. Chib, V.S., Rangel, A., Shimojo, S., and O'Doherty, J.P. (2009). Evidence for a common representation of decision values for dissimilar goods in human ventromedial prefrontal cortex. J. Neurosci. *29*, 12315–12320.
17. McClure, S.M., Berns, G.S., and Montague, P.R. (2003). Temporal prediction errors in a passive learning task activate human striatum. Neuron *38*, 339–346.
18. O'Doherty, J.P., Dayan, P., Friston, K., Critchley, H., and Dolan, R.J. (2003). Temporal difference models and reward-related learning in the human brain. Neuron *38*, 329–337.
19. Glascher, J., Hampton, A.N., and O'Doherty, J.P. (2009). Determining a role for ventromedial prefrontal cortex in encoding action-based value signals during reward-related decision making. Cereb. Cortex *19*, 483–495.
20. Rudebeck, P.H., Behrens, T.E., Kennerley, S.W., Baxter, M.G., Buckley, M.J., Walton, M.E., and Rushworth, M.F. (2008). Frontal cortex subregions play distinct roles in choices between actions and stimuli. J. Neurosci. *28*, 13775–13785.

Trinity College Institute of Neuroscience, Trinity College Dublin, Ireland.
E-mail: johnpodoherty@gmail.com

DOI: 10.1016/j.cub.2010.09.017