doi:10.1038/nature14066

Supplementary discussion

Gradual accumulation of evidence for or against different choices has been implicated in many types of decision-making, including value-based decisions[27-30], social decisions[31], economic decisions[32], gambling decisions[33], memory-based decisions[34], numerical comparison decisions[35], visual search decisions[7,9], and perceptual[1,6,8] decisions. It is therefore considered a core decision-making process. We developed a method that can estimate tuning curves for mentally-accumulated decision-making evidence in continuous-time throughout the decision process. In addition to helping to clarify the nature of the encoding in the many brain regions that have been reported to have firing rates correlated with accumulating evidence, our method can be applied to decision-making tasks beyond perceptual decision-making, and to measures of neural activity beyond spike rates.

Our rat study is closely related to previous studies in macaques. The method developed here for estimating tuning curves (neural firing rates as a function of accumulated evidence; Fig. 2) can also be applied in studies with human or non-human primates. Anatomical, neurophysiological, and causal manipulations suggest that rat PPC and FOF may be potential homologues of monkey PPC and FEF[12,13]. Wherever a direct comparison for accumulation of evidence could be made, our data from rat PPC and FOF are qualitatively similar to previous results in the corresponding regions in macaques (compare Fig. 1c to Fig. 7a of ref. [4], Fig. 1d to Fig. 3a of ref. [3], and Fig. 1e to Fig. 4 of ref. [16]). These striking similarities lead us to suggest that the rat results reported here (Figs. 1f, 2, 3, and 4, and Extended Data figures) will likely hold in non-human primates if analogous experiments were carried out, and that our main conclusions are likely to also hold for primate PPC and FEF. That prediction, however, remains to be tested.

We also found some clear differences with respect to non-human primates. These differences, however, were not directly related to accumulation of evidence, and it is unclear whether they have functional implications for how decisions based on accumulation of evidence are carried out in the different species. The most prominent of the differences are: (1) Neurons in primate PPC and FEF have predominantly contralateral

selectivity, whereas in rat PPC and FOF, neurons with contralateral and ipsilateral selectivity are roughly equally represented on each side of the brain. These rat data are consistent with similarly intermixed selectivity reported in simpler memory-guided orienting tasks in both rats[13] and mice[20,36]. (2) The latency to stimulus-selective responses in rat FOF is ~100 ms shorter than the latency to stimulus-selective responses in primate FEF[3].

The neuronal tuning curves for accumulated evidence in rat PPC revealed a veridical encoding of the graded value of the accumulated evidence that is similar to what was found in monkey PPC during a task that required the combination of probabilistic units of visual evidence in order to make a binary decision[17]. In that task, the evidence was presented sequentially but remained visible, so it allowed a strategy that does not involve the temporal accumulation. In contrast, our task does require temporal accumulation. Thus, our results bolster the conclusion that PPC veridically represents accumulated evidence when evidence is combined across time. Nevertheless, separate work from our laboratory suggests that PPC activity is not necessary for choice behavior in this task[18]. We speculate that PPC signals may instead be used for behavioral control that extends beyond the categorical left/right choice, such as in the computation of decision confidence[37,38].

With respect to decisions about where to orient to in space, previous studies have suggested that posterior parietal and prefrontal cortices play similar roles, and have similar neural encodings[3-5,8,11,19,39]. In contrast, for many other cognitive processes important distinctions between parietal and prefrontal cortices have been found. These processes include attentional control[40], sensorimotor rule selection[41], visual categorization[42-45], distractor suppression[46], working memory[47], and specifying spatial coordinate frames[48]. The contrast raises the question: why should spatial decision-making be different to those other cognitive processes? Our results suggest a resolution, by showing that when tuning curves are not plotted as a function of an external average stimulus, but as a function of an internal decision variable (the accumulated evidence), the encodings in PPC and FOF are now revealed to be distinct, with the FOF having a more categorical encoding. In other words,

our results suggest that spatial decision-making is *not* different to the other processes, in that even during spatial decision-making tasks, posterior parietal and prefrontal cortices *do* have distinct encodings.

In comparing posterior parietal and prefrontal contributions to cognitive tasks, a number of studies have examined the temporal transfer of the neural representation between the two areas[20,42-45]. Our results argue against a direct transfer of representations between PPC and FOF. In particular, the longer mean latency of PPC (~200 ms) compared to FOF (~100 ms) suggests that sensory information in this task may reach the FOF through circuits that bypass the PPC. Furthermore, the graded representation in PPC is unlikely to derive from the more categorical representation in FOF. We therefore speculate that both PPC and FOF may derive their representations from other circuit elements that themselves accumulate evidence, and that project to PPC and FOF. This raises the critical outstanding question of identifying the brain circuits that are responsible for evidence accumulation.

27. Basten, U., Biele, G., Heekeren, H. R. & Fiebach, C. J. How the brain integrates costs and benefits during decision making. *Proc. Natl. Acad. Sci. U.S.A.* **107,** 21767–21772 (2010).

28. Cavanagh, J. F. *et al.* Subthalamic nucleus stimulation reverses mediofrontal influence over decision threshold. *Nat. Neurosci.* **14,** 1462–1467 (2011).

29. Milosavljevic, M., Malmaud, J. & Huth, A. The drift diffusion model can account for value-based choice response times under high and low time pressure. *Judgment & Decision Making* **5,** 437–449 (2010).

30. Hunt, L. T. *et al.* Mechanisms underlying cortical activity during value-guided choice. *Nat. Neurosci.* **15,** 470–476 (2012).

31. Krajbich, I., Lu, D., Camerer, C. & Rangel, A. The attentional drift-diffusion model extends to simple purchasing decisions. *Front Psychol* **3,** 193 (2012).

32. Gluth, S., Rieskamp, J. & Büchel, C. Deciding when to decide: time-variant sequential sampling models explain the emergence of value-based decisions in the human brain. *J. Neurosci.* **32,** 10686–10698 (2012).

33. Busemeyer, J. R. in *Time pressure and stress in human judgment and and decision making* 181–193 (Springer, 1993). doi:10.1007/978-1-4757-6846-6_13

34. Ratcliff, R. A theory of memory retrieval. *Psychol Rev* **85,** 59–108 (1978).

35. Sigman, M. & Dehaene, S. Parsing a cognitive task: a characterization of the mind's bottleneck. *PLoS Biol.* **3,** e37 (2005).

36. Harvey, C. D., Coen, P. & Tank, D. W. Choice-specific sequences in parietal cortex during a virtual-navigation decision task. *Nature* **484,** 62–68 (2012).

37. Kiani, R. & Shadlen, M. N. Representation of confidence associated with a decision by neurons in the parietal cortex. *Science* **324,** 759–764 (2009).

38. Kepecs, A., Uchida, N., Zariwala, H. A. & Mainen, Z. F. Neural correlates, computation and behavioural impact of decision confidence. *Nature* **455,** 227–231 (2008).

39. Chafee, M. V. & Goldman-Rakic, P. S. Matching patterns of activity in primate prefrontal area 8a and parietal area 7ip neurons during a spatial working memory task. *J. Neurophysiol.* **79,** 2919–2940 (1998).

40. Buschman, T. J. & Miller, E. K. Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices. *Science* **315,** 1860–1862 (2007).

41. Gail, A., Klaes, C. & Westendorff, S. Implementation of spatial transformation rules for goal-directed reaching via gain modulation in monkey parietal and premotor cortex. *J. Neurosci.* **29,** 9490–9499 (2009).

42. Merchant, H., Crowe, D. A., Robertson, M. S., Fortes, A. F. & Georgopoulos, A. P. Top-Down Spatial Categorization Signal from Prefrontal to Posterior Parietal Cortex in the Primate. *Front. Syst. Neurosci.* **5,** (2011).

43. Swaminathan, S. K. & Freedman, D. J. Preferential encoding of visual categories in parietal cortex compared with prefrontal cortex. *Nat. Neurosci.* **15,** 315–320 (2012).

44. Goodwin, S. J., Blackman, R. K., Sakellaridi, S. & Chafee, M. V. Executive Control Over Cognition: Stronger and Earlier Rule-Based Modulation of Spatial Category Signals in Prefrontal Cortex Relative to Parietal Cortex. *J. Neurosci.* **32,** 3499–3515 (2012).

45. Crowe, D. A. *et al.* Prefrontal neurons transmit signals to parietal neurons that reflect executive control of cognition. *Nat. Neurosci.* **16,** 1484–1491 (2013).

46. Suzuki, M. & Gottlieb, J. Distinct neural mechanisms of distractor suppression in the frontal and parietal lobe. *Nat. Neurosci.* **16,** 98–104 (2013).

47. Qi, X.-L. Comparison of neural activity related to working memory in primate dorsolateral prefrontal and posterior parietal cortex. *Front. Syst. Neurosci.* (2010). doi:10.3389/fnsys.2010.00012

48. Pesaran, B., Nelson, M. J. & Andersen, R. A. Dorsal premotor neurons encode the relative position of the hand, eye, and goal during reach planning. *Neuron* **51,** 125–134 (2006).