TABLE 1 Isotope data for Macdonald seamount

Th (p.p.m.)	4.3 ± 0.3	Th/U	2.6 ± 0.5
U (p.p.m.)	1.7 ± 0.1	$[Th/U]_s$	2.1 ± 0.2
(^{238}U)	1.25 ± 0.07	$(^{230}Th/^{232}Th)$	1.5 ± 0.1
(^{234}U)	1.30 ± 0.07	$(^{234}U/^{238}U)$	1.04 ± 0.06
(^{232}Th)	1.04 ± 0.05	$(^{230}Th/^{238}U)$	1.2 ± 0.1
(^{230}Th)	1.5 ± 0.1	$(^{226}Ra/^{230}Th)$	1.12 ± 0.09
(^{226}Ra)	1.70 ± 0.07	$(^{210}Po/^{226}Ra)$	0.84 ± 0.08
(^{210}Pb)	1.4 ± 0.1	$(^{210}Po/^{210}Pb)_i$	0.01 ± 0.04
$(^{210}Po)_{sw}$	66 ± 20	$^{144}Nd/^{143}Nd$	0.51283 ± 0.00001
$(^{210}Po)_{slk}$	970 ± 65	$^{87}Sr/^{86}Sr$	0.70366 ± 0.00003

Activities (in d.p.m. g^{-1}) and activity ratios of U-series nuclides in fresh Macdonald seamount basalt. U and Th isotopes were measured by high-resolution alpha spectrometry (see, for example, ref. 31). (^{226}Ra) was measured by the ^{222}Rn-emanation method (see. for example, ref. 36). $(^{210}Po)_{sw}$ is the average initial activity (d.p.m. dm^{-3}) in seawater collected during the 11 October 1987 eruption based on measurements made on 2 February and 23 February 1988. $(^{210}Po)_{slk}$ is the initial activity in slick material collected during the 1 February 1989 eruption based on a single measurement made on 13 June 1989. Sr and Nd isotopic ratios were measured by thermal-ionization mass spectrometry. Th/U is the value observed in the rock and $[Th/U]_s$ is the source value calculated from $(^{230}Th/^{232}Th)$.

independent of any volcanic ash component. The occurrence of such horizons could help provide dates for alkalic magmatic activity at now dormant volcanoes, for example along a hot-spot seamount chain.

In addition to the isotopes already discussed, we measured other U-series nuclides (Table 1) which help to characterize the volcanism at Macdonald. We note that the activity ratios $(^{226}Ra/^{230}Th)$ and $(^{230}Th/^{238}U)$ are within the range of values for other ocean island basalts (OIB) (refs 26, 27 and our unpublished data); the ^{226}Ra excess constrains the crustal residence time of the magma to $\leq 8{,}000$ yr, and $(^{230}Th/^{232}Th)$ is high and considered in isolation, implies a low value (~ 2.1) of Th/U in the source. This is more similar to values characteristic of the mid-ocean-ridge basalt (MORB) source than of the OIB source (refs 26, 28-31). On the Th-Sr isotope diagram, the Macdonald seamount datum falls far above the broad array defined by oceanic rocks[32], suggesting that either the Sr or Th isotopic ratios have been affected by secondary processes. Comparison of our Macdonald seamount Sr and Nd data (Table 1) with those from other nearby eastern Austral-Cook islands[24,33] suggests that $^{87}Sr/^{86}Sr$ is indeed high for the measured Nd isotopic composition and that the source Sr isotopic ratio may be closer to 0.7028. If this is so, the Sr-Th isotope correlation indicates that $(^{230}Th/^{232}Th)$ should be close to 1.25, considerably lower than the measured value but still far above the OIB range, indicating a truly depleted source for Macdonald.

The process most likely to cause the secondary isotope shifts is the incorporation of altered oceanic crustal materials, because both U concentration (and hence ^{230}Th) and $^{87}Sr/^{86}Sr$ increase during alteration. To change $^{87}Sr/^{86}Sr$ from 0.7028 to 0.7073 and $(^{230}Th/^{232}Th)$ from 1.25 to 1.5 would require about 14% of the Sr and 17% of the ^{230}Th to come from the alteration component. Similar processes have been postulated to occur at other localities (for example, Kiluea[34] and Iceland[35]). Furthermore, the frequent explosive magmatism, the observed release of large quantities of gas during recent eruptions, and the presence of scoriaceous spatter cones at the summit suggest that Macdonald is presently erupting highly gas-charged lavas. This implies a large increase of gas pressure over a short time interval to permit rapid gas build-up and is consistent with the effective sealing of chamber-to-surface magma conduits by seawater circulation through the crust between eruptions. □

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1. Norris, A. & Johnson, R. H. *J. geophys. Res.* **74,** 650-664 (1968).
2. Geophysical Events, *Trans. Am. geophys. Un.* **170,** 163 (1989).
3. McNutt, M. K. & Fischer, K. M. in *Seamounts, Islands, and Atolls* (eds Keating, B. H., Fryer, P., Batiza, R. & Boehlert, G. W.) AGU geophys. monograph **43,** 23-34 (Washington, DC, 1987).
4. McDougall, I. & Duncan, R. A. *Tectonophysics* **63,** 276-295 (1980).
5. Turner, D. L. & Jarrard, R. D. *J. Volcan. geotherm. Res.* **12,** 187-220 (1982).
6. Talandier, J. & Okal, E. A. *Geophys. Res. Lett.* **1,** 813-816 (1984).
7. Johnson, R. H. *Nat. Geogr. Soc. Res. Rep.* **12,** 389-405 (1980).
8. Wyart, J. *C. r. hebd. Séanc. Acad. Sci., Paris* **290,** 1055-1057 (1980).
9. Bennett, J. T., Krishnaswami, S., Turekian, K. K., Melson, W. G. & Hopson, C. A. *Earth. planet. Sci. Lett.* **60,** 61-69 (1982).
10. Gill, J., Williams, R. & Bruland, K. *Geophys. Res. Lett.* **12,** 17-20 (1985).
11. Lambert, G., Le Cloarec, M. F., Ardouin, B. & Le Roulley, J. C. *Earth planet. Sci. Lett.* **76,** 185-192 (1985/86).
12. Lambert, G., Bristeau, P. & Polian, G. *Geophys. Res. Lett.* **3,** 724-726 (1976).
13. Vilenskiy, V. D. *Geochem. Int.* **14,** 14-19 (1977).
14. Polian, G. & Lambert, G. *J. Volcan. geotherm. Res.* **6,** 125-137 (1979).
15. Lambert, G., Ardouin, B. & Polian, G. *J. geophys. Res.* **87,** 11,103-11,108 (1982).
16. Nevissi, A. E. *J. geophys. Res.* **89,** 6326-6328 (1984).
17. Le Cloarec, M. F., Lambert, G., Le Roulley, J. C. & Ardouin, B. *J. Volcan. geotherm. Res.* **28,** 85-89 (1986).
18. Koide, M. & Bruland, K. W. *Analytica chim. Acta* **75,** 1-19 (1975).
19. Kadko, D., Bacon, M. P. & Hudson, A. *Earth planet. Sci. Lett.* **81,** 349-357 (1986/87).
20. Buat-Ménard, P. & Arnold, M. *Geophys. Res. Lett.* **5,** 245-248 (1978).
21. Zoller, W. H. *et al. Science* **222,** 1118-1121 (1983).
22. Lambert, G., Le Cloarec, M. F. & Pennisi, M. *Geochim. cosmochim. Acta* **52,** 39-42 (1988).
23. Pennisi, M., Le Cloarec, M. F., Lambert, G. & Le Roulley, J. C. *Earth planet. Sci. Lett.* **88,** 284-288 (1988).
24. Nakamura, Y. & Tatsumoto, M. *Geochim. cosmochim. Acta* **52,** 2909-2924 (1988).
25. Nriagu, J. O. & Pacyna, J. M. *Nature* **333,** 134-138 (1988).
26. Newman, S., Finkel, R. C. & Macdougall, J. D. *Geochim. cosmochim. Acta* **48,** 315-324 (1984).
27. Krishnaswami, S., Turekian, K. K. & Bennett, J. T. *Geochim. cosmochim. Acta* **48,** 505-511 (1984).
28. Condomines, M., Morand, P. & Allègre, C. J. *Earth planet. Sci. Lett.* **55,** 247-256 (1981).
29. Newman, S., Finkel, R. C. & Macdougall, J. D. *Earth planet. Sci. Lett.* **65,** 17-33 (1983).
30. Rubin, K. H. & Macdougall, J. D. *Nature* **335,** 158-161 (1988).
31. Tanzer, M. O. thesis, Univ. California-San Diego (1985).
32. Condomines, M., Hemond, C. H. & Allègre, C. J. *Earth planet. Sci. Lett.* **90,** 243-262 (1988).
33. Vidal, Ph., Chauvel, C. & Brousse, R. *Nature* **307,** 536-538 (1984).
34. Condomines, M., Bernat, M. & Allègre, C. J. *Earth planet. Sci. Lett.* **33,** 122-125 (1976).
35. Hemond, C. H. *et al. Earth planet. Sci. Lett.* **87,** 273-285 (1988).
36. Broecker, W. S. in *Symp. Diffusion in Oceans and Fresh Waters* (ed. Ichiyes, T.) 114-115 (Lamont-Doherty Geologic Observatory, Palisades, New York, 1965).
37. Flynn, W. W. *Analytica chim. Acta* **43,** 221-227 (1968).

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Neuronal correlates of a perceptual decision

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THE relationship between neuronal activity and psychophysical judgement has long been of interest to students of sensory processing. Previous analyses of this problem have compared the performance of human or animal observers in detection or discrimination tasks with the signals carried by individual neurons, but have been hampered because neuronal and perceptual data were not obtained at the same time and under the same conditions[1-4]. We have now measured the performance of monkeys and of visual cortical neurons while the animals performed a psychophysical task well matched to the properties of the neurons under study. Here we report that the reliability and sensitivity of most neurons on this task equalled or exceeded that of the monkeys. We therefore suggest that under our conditions, psychophysical judgements could be based on the activity of a relatively small number of neurons.

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Our general methods for monitoring unit activity and eye position in alert, behaving monkeys are derived from those devised by Wurtz *et al.*[5] and our psychophysical methods were based on those described by Newsome and Paré[6]. In brief, animals were trained to report the direction of motion of a random dot display in which some dots moved coherently while the remainder moved at random. We varied the strength of the motion signal by varying the proportion of the dots moving coherently: at 0% correlation, all the motion was random; at 100% correlation, all the motion was coherent. Near threshold, the stimulus resembled the dynamic noise seen on a domestic television set tuned between stations, combined with a barely perceptible sensation of global motion. We recorded single-neuron activity from area MT (V5), a region of the extrastriate visual cortex concerned with motion processing, where most neurons respond optimally to visual stimuli of a particular direction and speed of motion[7-10]. Because efficient extraction of motion signals from this stimulus requires considerable integration over space, it seemed likely that neurons in MT, which have relatively large receptive fields, would be particularly suited to this task. Newsome and Paré[6] have recently shown that lesions of MT elevate perceptual thresholds for this task.

We used a two-alternative forced-choice procedure to measure thresholds. We placed our stimulus so that it just covered the receptive field of the neuron under study, and adjusted the speed to match that preferred by the neuron. Motion was presented either in the neuron's preferred direction or in the 'null' direction 180° away. On an individual trial, the monkey was required to hold fixation for 2 seconds while the motion stimulus was presented. At the end of the trial, the monkey indicated his judgment by transferring his gaze to one of two small light-emitting diodes, corresponding to the preferred or null direction of motion. We presented at least 30 trials (15 in each direction) for each of several correlation values chosen to elicit performance that varied from chance to near perfection, and compiled these data into psychometric functions. Recalling that performance would be 50% correct by chance, we defined the threshold as the correlation required for the monkey to judge the direction of motion correctly on 82% of the trials.

While measuring the psychophysical threshold, we recorded the activity of the MT neuron for which the stimulus parameters were optimized. The computer counted the action potentials elicited on each trial, and compiled distributions like those shown for a typical neuron in Fig. 1*a*. In these distributions, filled bars represent trials in which the motion was in the null direction, and cross-hatched bars indicate trials for the preferred direction. It is evident that at a correlation of 0.8% the two distributions were not different, whereas at a correlation of 12.8%, where the neuron was strongly direction-selective, they barely overlapped. To compare these neuronal data with the psychophysical data, we postulated that performance depended on a comparison between the activity of two neurons, the one under study and another differing only in that it preferred the opposite direction of motion. Under this assumption, we could use the distributions in Fig. 1*a* to represent the responses of the neuron under study and its 'antineuron'; we simply reversed the preferred and null directions for the antineuron. On any individual trial, therefore, the observer would compare a response drawn from the distribution represented by the hatched bars in Fig. 1*a* with one drawn from the distribution represented by the solid bars. The direction chosen would be the preferred direction of the neuron giving the larger response. The performance of an MT neuron could then be characterized as the probability that a randomly selected response from the hatched distribution in Fig. 1*a* was larger than a randomly selected response from the solid distribution. We chose this method for analysing physiological data because it most directly related neuronal performance to the directional discrimination task that the monkey was engaged in.

For the data in Fig. 1*a*, at a correlation of 0.8%, this decision rule chose the correct direction only on about half the trials (random performance), whereas at a correlation of 12.8% it performed nearly perfectly. We used a method based on signal detection theory[11] to estimate this choice probability for each correlation value, and plotted the results as 'neurometric functions' formally equivalent to the psychometric functions representing the psychophysical data[2,4]. The two functions for this example neuron are shown in Fig. 1*b*; filled circles represent neurometric data, open circles represent psychometric data. Evidently the two curves are very similar, with the neurometric

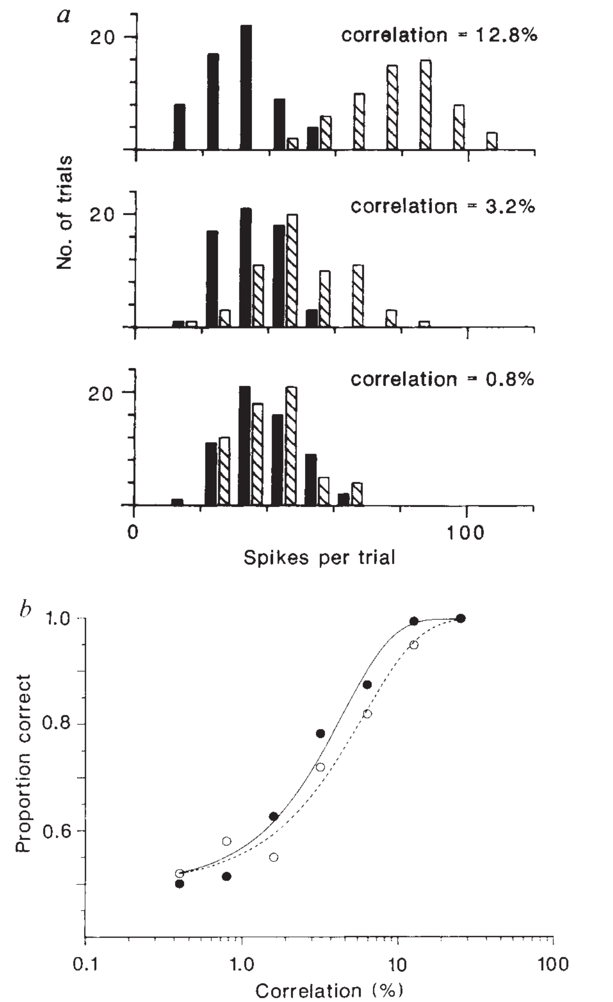

FIG. 1 Physiological and psychophysical data obtained simultaneously from a rhesus monkey. *a*, The responses of a directionally selective MT neuron at three different motion correlations spanning physiological threshold. The hatched bars represent responses to motion in the neuron's preferred direction; the solid bars indicate responses to motion in the null direction (180° opposite to the preferred). Sixty trials were performed in each direction for each of the three correlation levels. Response distributions for a range of correlation levels were used to compute a 'neurometric' function that characterized the neuron's sensitivity to the motion signal and could be compared with the psychometric function computed from the monkey's behavioural responses. *b*, Comparison of simultaneously recorded psychometric and neurometric functions. Psychophysical performance of the monkey, ○; performance of the neuron, ●. Psychophysical performance at each correlation is given by the proportion of trials on which the monkey correctly identified the direction of motion. Neuronal performance is calculated from distributions of responses like those in Fig. 1*a*, using a signal-detection method described in the text. The physiological and psychophysical data form similar curves, but the data for the neuron lie to the left of the data for the monkey, meaning that the neuron was somewhat more sensitive than the monkey. We fit the data with smooth functions of the form introduced to psychophysics by Quick[12]. Threshold, defined as the correlation for which the direction of motion was identified correctly on 82% of the trials, was 6.1% for the monkey and 4.4% for the neuron.

data points lying slightly to the left of the psychometric data points; in this case the neuronal threshold was slightly lower than the psychophysical one. We used a likelihood-ratio statistic to test the hypothesis that the psychometric and neurometric functions were the same. For this neuron, this hypothesis could not be rejected ($P > 0.05$).

We performed this analysis for 45 neurons recorded from one monkey, and 15 neurons from a second. Figure 2 shows a histogram of the distribution of the ratio of neurometric to psychometric thresholds for these 60 neurons. Values of this ratio of <1 represent cases where the neuron's threshold was lower than the monkey's; values >1 represent cases where the monkey's performance was better than the neuron's. Intuitively, it might be expected that the behavioural threshold would be lower than any particular neuronal threshold but, in most cases, neuronal thresholds and perceptual thresholds were similar. Indeed in some cases, neuronal thresholds were substantially *lower* than perceptual thresholds. For 20 of the 60 neurons in our sample, the psychometric and neurometric functions were statistically indistinguishable ($P > 0.05$); in 18 of the 40 remaining cases, neuronal thresholds were lower than perceptual thresholds. In other words, if the monkeys were able to select and measure the discharge of some of these neurons as we did, their performance could have been better than it actually was.

An inability to select the most informative signals can be considered as a kind of perceptual uncertainty, of the kind modelled by Pelli[13]. Obliged to monitor signals from many sources less informative than the one perfectly tuned to the visual target, the animal's perceptual performance would be degraded, because each sub-optimal source would contribute more noise than signal. Neuronal performance would then exceed psychophysical performance. Our results suggest, however, that this effect is not large. Substantial uncertainty would make the psychometric function steeper than the neurometric function[13], but as was the case for the example shown in Fig. 1*b*, the slopes of these two functions are usually similar. We thus conclude that under our conditions, the monkey's perceptual decision is not greatly affected by irrelevant signals introduced by uncertainty.

The apparent absence of uncertainty leads, however, to another question: if a perceptual decision can be based with relative certainty on the discharge of the most informative neurons, why is behavioural performance not further enhanced by using a pooled signal derived from many such informative neurons? If enough such neurons were present, such pooling would substantially improve psychophysical performance by averaging out the noise that obscures weak signals. Our data show that in most cases, the neuronal and psychophysical performances are similar, indicating that signals from many neuronal sources are not pooled to reduce perceptual thresholds.

One way to account for the absence of either pooling or uncertainty effects is to suggest that the variability in the responses of similarly tuned neurons is correlated. Both pooling and uncertainty act as we have stated only if different neuronal signals are perturbed by *independent* sources of variation. If the sources are not independent, then uncertainty does no damage and pooling provides no benefit, because different neurons are carrying similar signals. The rich network of shared connections that link MT neurons with the retina might well produce correlation among neurons with related selectivities, but this possibility has not been studied. Our lack of information about the degree of shared variability makes it impossible for us to assert that the neurons whose responses we have recorded are the ones that contribute to the monkey's perceptual judgements. Nonetheless, our results show that a reasonable account of the monkey's performance can be constructed, using a simple decision rule, from signals carried by small numbers of neurons whose selectivities are well matched to the demands of the perceptual task. □

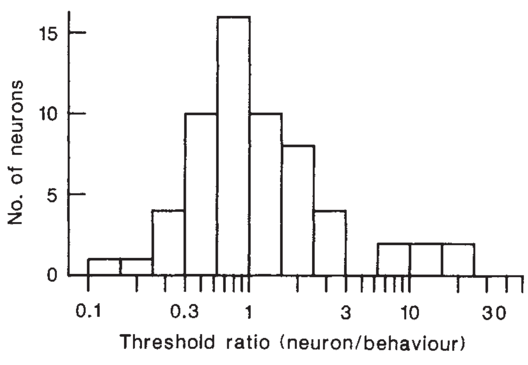

FIG. 2 Comparison of psychophysical and physiological thresholds obtained for 60 MT neurons in two rhesus monkeys. The frequency histogram shows the distribution of the ratio of the physiological threshold to the psychophysical threshold for all the neurons for which we obtained data. A value of 1 represents perfect correspondence between psychophysical and physiological thresholds; values <1 indicate that the physiological threshold was lower than the psychophysical threshold, whereas values >1 indicate the converse. The directional preferences of the 60 neurons were roughly uniformly distributed, and there was no reliable association between a neuron's direction or speed preference and its threshold relative to the perceptual threshold.

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1. Barlow, H. B. & Levick, W. R. *J. Physiol.* **200,** 1–24 (1969).
2. Tolhurst, D. J., Movshon, J. A. & Dean, A. F. *Vision Res.* **23,** 775–785 (1983).
3. Parker, A. J. & Hawken, M. J. *J. opt. Soc. Am.* **A2,** 1101–1114 (1985).
4. Bradley, A., Skottun, B. C., Ohzawa, I., Sclar, G. & Freeman, R. D. *J. Neurophysiol.* **57,** 755–772 (1987).
5. Mikami, A., Newsome, W. T. & Wurtz, R. H. *J. Neurophysiol.* **55,** 1308–1327 (1986).
6. Newsome, W. T. & Paré, E. B. *J. Neurosci.* **8,** 2201–2211 (1988).
7. Dubner, R. & Zeki, S. M. *Brain Res.* **35,** 528–532 (1971).
8. Zeki, S. M. *J. Physiol.* **236,** 549–573 (1974).
9. Maunsell, J. H. R. & Van Essen, D. C. *J. Neurophysiol.* **49,** 1127–1147 (1983).
10. Albright, T. D. *J. Neurophysiol.* **52,** 1106–1130 (1984).
11. Green, D. M. & Swets, J. A. *Signal Detection Theory and Psychophysics.* (Wiley, New York, 1966).
12. Quick, R. F. *Kybernetik* **16,** 65–67 (1974).
13. Pelli, D. G. *J. opt. Soc. Am.* **A2,** 1508–1532 (1985).

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Hippocampal abnormalities in amnesic patients revealed by high-resolution magnetic resonance imaging

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THE identification of brain structures and connections involved in memory functions has depended largely on clinico-pathological studies of memory-impaired patients[1–4], and more recently on studies of a primate model of human amnesia[5,6]. But quantitative neurobehavioural data and detailed neuropathological information are rarely available for the same patients[7–9]. One case has demonstrated that selective bilateral damage to the hippocampus causes a circumscribed memory impairment in the absence of other intellectual deficits[9]. This finding, in conjunction with evidence from humans[10,11] and monkeys[12–16], indicates that the hippocampus together with adjacent and anatomically related structures is essential for the formation of long-term memory, perhaps by virtue of