

## Huxley versus Owen: the hippocampus minor and evolution

Charles G. Gross

*In Victorian Britain a major debate over evolution raged between Thomas H. Huxley and Richard Owen. The central issue between them was whether or not the human brain was unique in having a hippocampus minor (also known as the calcar avis), a posterior horn and a posterior lobe.*

For much of the 19th century, evolution and its implications were hotly debated in Britain. At the beginning of the century the French zoologist Jean-Baptiste Lamarck had proposed an evolutionary process that began with the simplest organisms and 'progressed' through apes to man<sup>1</sup>. Lamarck's ideas appealed to the left of the day, such as working-class organizers, middle-class Dissenters and medical radicals and reformers, who were attracted by his materialism and deism. They used his idea that biological evolution implies progress and improvement to demand social evolution and social progress such as the end of privileges of the established church, the introduction of universal suffrage, reform of medical care, education for women and similar radical reformist notions<sup>2,3</sup>. Lamarck's 'progressive' notion of evolution became widespread in Britain through its popularization in Robert Chambers' best-selling *Vestiges of Creation*, which was published anonymously to avoid persecution and prosecution for blasphemy and related crimes<sup>3-5</sup>.

The conservative Oxbridge scientist-clergymen who dominated early Victorian science saw Lamarckism and its spread by *Vestiges* as a direct threat to the established order of Church and State. Adam Sedgewick, Professor of Geology at Cambridge and President of the Geological Society, described the book as 'a filthy abortion' that '...breaks down the barriers between right and wrong... undermines the whole moral and social fabric... and [implies] religion is a lie; human law is a mass of folly... morality is moonshine... our labours for the black people of Africa the works of madmen'<sup>3,6</sup>.

### Owen uses neuroanatomy to separate man and ape

The leading zoologist to combat the bestialization of man, implied by evolutionary ideas and their threat to the established order, was Prof. (later Sir) Richard Owen. By the middle of the century Owen was England's leading paleontologist and anatomist. He was also socially and politically very well connected – he dined with princes and prime ministers and lectured on zoology to the Royal children. His political conservatism was not only theoretical: when the radical Chartists were thought to threaten London with their militant marches and violent demonstrations, he joined the militia of urban gentry to defend, literally, the status quo<sup>7,8</sup>.

In 1858, probably spurred by the impending publication of *The Origin of Species*, Owen published a new classification of mammals designed to

build a wall between ape and man<sup>9</sup>. He placed man apart from all other primates, not merely in a separate order but in a separate subclass. He did so on three anatomical criteria, all of them concerning the brain. The first fundamental brain difference between humans and animals claimed by Owen was that only man has the 'posterior lobe' (i.e. the part of the cerebrum extending beyond the cerebellum). The second difference was that only humans have a posterior horn in their lateral ventricles. The third and most important difference was that only man has a hippocampus minor.

### What is the hippocampus minor?

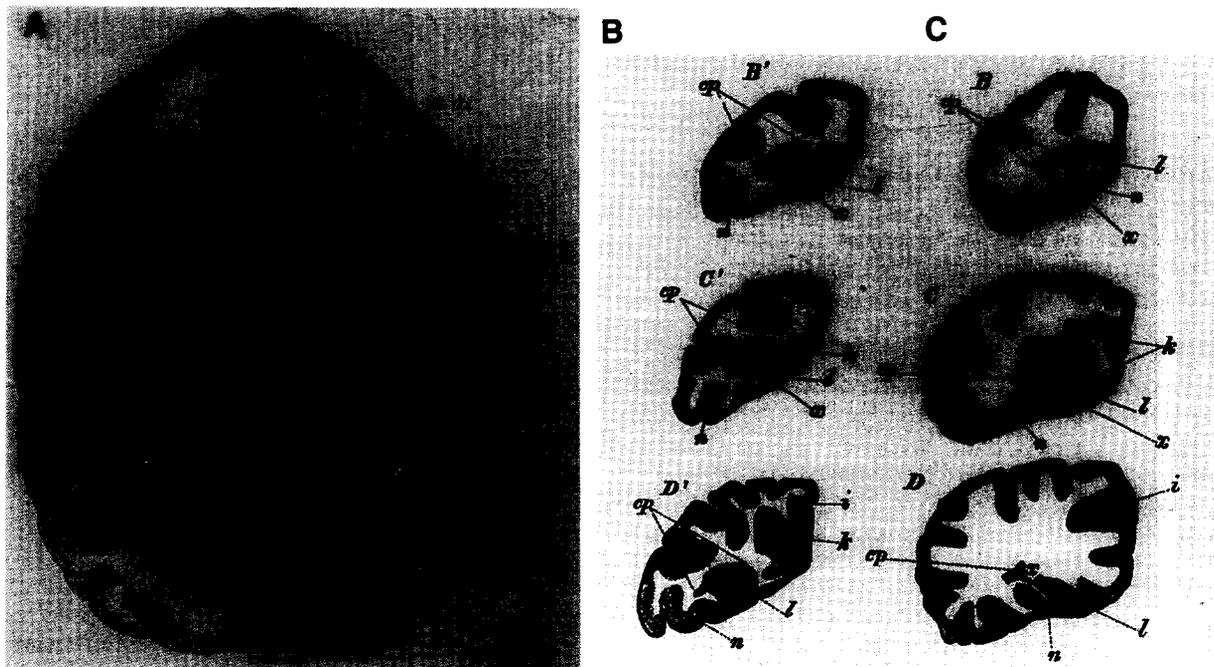
The hippocampus minor is a ridge in the floor of the posterior horn of the lateral ventricle caused by the deep inward penetration of the calcarine fissure (Fig. 1). The original term for this structure was 'calcar avis' (Latin for cock's spur, which it resembles) and this is the term that is current today. In 1786, when Vicq d'Azyr systematized brain nomenclature, he changed the name of the calcar avis to 'hippocampus minor' and, in parallel, he also changed the name of the hippocampus, the larger ridge in the floor of the ventricle, to 'hippocampus major'.

In considering Owen's neuroanatomical criteria for humanity, it is useful to remember that in the mid-19th century virtually nothing was known about the localization of higher functions in the brain. Gall's extreme phrenological localization was deadlocked with Flourens' extreme holism; Broca's localization of language in the frontal lobe had to wait until 1861, and Fritsch and Hitzig's discovery of the electrical excitability of motor cortex until 1870 (Refs 11,12).

Owen's choice of two ventricular structures appears to have been a persistence of the importance Galen had given the ventricles in his physiological system 17 centuries earlier. His description of the ventricles was quite accurate but the early church fathers, particularly Nemesius, Bishop of Emesa, radically altered his conceptions of their structure and function. They transformed the ventricles into three more-'perfect' spheres. Galen had localized sensory and motor functions in the solid portions of the cerebrum. The church fathers, however, were looking for a less mundane site for the interaction of the body and soul. For this purpose they chose the 'empty' spaces in the brain that Galen had described – the ventricles. They then took the aristotelian faculties of the mind – sensation, cognition and memory – and located them in the anterior, middle and posterior ventricles, respectively<sup>11</sup>. Drawings showing this ventricular localization of mental function hardly changed for over a thousand years, except for the expressions on the faces<sup>13</sup>.

When systematic brain dissection began again in the Renaissance the brains were usually dissected

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**Fig. 1.** The hippocampus minor (X) and other structures, in a horizontal dissection of the brain of the spider monkey (A) and in sections through its brain (B) and that of a human (C). Abbreviations: ca, anterior cornu; cd, descending cornu; cp, posterior cornu; i, calloso-marginal sulcus; k, occipito-parietal sulcus; l, calcarine sulcus; n, collateral sulcus<sup>10</sup>.

from the top down, often *in situ*. As in the famous plates of Vesalius, ventricular structures were carefully depicted and labeled because of their importance in Galenic theory. In contrast, the cortex was usually drawn in a schematic fashion, since, at least until Gall and phrenology<sup>12</sup>, it was usually thought to be unimportant. The theoretical importance of the ventricles persisted presumably because no better theory of brain function emerged, and better ideas, not facts, are required to overturn a theory. Given this tradition, it is not surprising that Owen, looking for important and 'higher' parts of the human brain, looked to the ventricles<sup>13</sup>.

Owen's other criterion, that the cerebrum covers the cerebellum only in man (the posterior lobe) had two roots<sup>13</sup>. The first was that the cerebrum expands posteriorly (and anteriorly) as one ascends the phylogenetic scale, reaching a maximum in humans. (However, it does extend beyond the cerebellum in apes as well as humans.) The second was that at the time of Owen's classification paper, ape brains were relatively rare and there were several published illustrations of them showing an exposed cerebellum in a dorsal view, apparently the result of removing unfixed brains.

**The bulldog grows his teeth . . .**

As soon as T. H. Huxley learned of Owen's new primate classification scheme he saw his opportunity to 'nail . . . [Owen] . . . that mendacious humbug . . . like a kite to the barn door'<sup>8</sup>. Huxley, 21 years junior to Owen, had a history of intense acrimony with him. As a junior researcher, Huxley had often asked Owen for letters of recommendation for jobs and grants. Four days after writing another such request to Owen and not yet receiving an answer, the two met on the street and Huxley wrote of the incident

to a friend in a manner that epitomizes the personalities of the junior and senior scientists: 'Of course I was in a considerable rage . . . I was going to walk past, but he stopped me, and in the blandest and most gracious manner said, "I have received your note. I shall grant it." The phrase and the implied condescension were quite 'touching', so much that if I stopped for a moment longer I must knock him into the gutter. I therefore bowed and walked off'<sup>8</sup>.

Owen sent the recommendation a few days later and Huxley got his research funds. Yet, in this period Huxley repeatedly attacked Owen, but only privately; for example he wrote that he 'felt it necessary always to be on guard against him' and that Owen was blocking publication of his papers<sup>14</sup>.

In 1854, Huxley got a position teaching natural history at the Government School of Mines, a post he kept for another 30 years, eventually turning down chairs at Oxford and Harvard, among other places. No longer needing job references from Owen, Huxley's attacks on him became more public and vitriolic and Owen answered in kind. The issues covered much of contemporary zoology; from the presence of an anus in particular brachiopods to Owen's Platonic-Naturphilosophie theory of archetypes, the idea that there was a basic pattern to which all vertebrates conformed<sup>13-15</sup>.

Although scientific controversy tended to be more openly nasty in Victorian England than today, the Owen-Huxley antagonism was extreme, even by standards of the time and it had far from peaked. Huxley's youthful arrogance, hot temper, and anti-clericalism, and Owen's stubbornness, superciliousness and religiosity, served to exaggerate their scientific differences. The fact that both came from lower middle-class backgrounds, and Owen eagerly

sought while Huxley tended to resist social ascent, probably further exacerbated their differences<sup>7,8,13,14</sup>.

By the end of the 1850s, Huxley had embraced the idea of evolution and what it implied about mankind. In contrast, Owen, after showing some (quiet)-sympathy for *Vestiges*, moved to a strongly anti-evolutionary position, both because of the political and religious implications and his wont for a 'if it's not my idea it's no good' stance<sup>16</sup>.

Soon after the publication of *The Origin of Species* in 1860, the British Association for the Advancement of Science, the 'parliament of science', met in Oxford. On the opening day of the meeting, Owen presented his view that the brain of the gorilla was more different from that of man than from that of the lowest primate because only man had a posterior lobe, a posterior horn, and a hippocampus minor; hence the descent of man from the apes, a crucial implication of Darwin's ideas, was impossible. In response, Huxley made a 'direct and unqualified contradiction' of Owen and promised to support his arguments in detail elsewhere<sup>14,17</sup>. He did so, repeatedly, over the next three years.

Two days later, Samuel Wilberforce, Bishop of Oxford (who was nicknamed 'Soapy Sam' from his slippery debating style), having been briefed by Owen, attacked Darwin and evolution. Then, turning to Huxley and referring to his earlier clash with Owen over brain anatomy and human kinship, 'he begged to know was it through his grandfather or his grandmother that he claimed descent from a monkey?' Huxley responded by defending vigorously Darwin's theory and concluded with the most famous repartee in the history of science, that 'he was not ashamed to have a monkey for his ancestor; but he would be ashamed to be connected with a man who used great gifts to obscure the truth'<sup>14,18</sup>.

Years later, the exchange between Huxley and Wilberforce took on an exaggerated mythical existence. At the time, however, Wilberforce, as well as Huxley, believed himself the victor. Furthermore, Darwin's friend, the plant geographer J. D. Hooker, who spoke last in the session, thought he, rather than Huxley, had demolished Wilberforce. A reporter present summarized it all as 'uncommonly lively'<sup>17,18</sup>.

### ... and attacks and attacks

As soon as he had read Owen's new classification scheme, Huxley began systematically to dissect monkey brains. He soon realized the magnitude of Owen's errors. He wanted to do more than prove Owen wrong. He wanted to prove him dishonest and thereby eliminate the leading opponent of Darwin in the scientific community. Huxley grasped the hippocampus minor as the vehicle to do so<sup>13,24</sup>.

After the initial challenge at the Oxford meeting, Huxley began the campaign against Owen in the *Natural History Review*, a journal he had just founded as a pro-Darwin and anti-clerical organ. The first issue opened with his own attack on Owen's three criteria for the uniqueness of man, with a barrage of citations and personal communications testifying that infra-human primates pos-

essed a posterior lobe, a posterior horn and above all a hippocampus minor, proportionally as big or bigger than in man<sup>19</sup>. Huxley put great emphasis on quoting sources that Owen must have known about and that in failing to mention them was 'guilty of wilful and deliberate falsehood'. At the end of his paper, Huxley readily admitted that there are differences between the human brain and that of the higher apes such as size, the relative proportions of different parts, and the complexity and number of convolutions, but that these are 'of no very great value' because they are the same as those between the brains of the 'highest' and 'lowest' human races 'though more in degree'. In any case, he concludes, the brains of monkeys 'differ far more widely from the brain of an orang than the brain of an orang differs from that of man' and, therefore, Owen's dividing of man from ape by cerebral characters is wrong.

The first two volumes of the *Natural History Review* had another five major articles attacking Owen's anatomical claims<sup>13</sup>. One of the articles was on the orang-utang brain by George Rolleston<sup>20</sup>, who had won the Chair of Anatomy at Oxford, with Huxley's help, over a candidate of Owen's. It placed great emphasis on showing the cerebrum covering the cerebellum, a posterior horn and hippocampus minor present in both orang and human. Rolleston noted that as he was not a 'materialist' these similarities of the brains of men and apes were, in any case, irrelevant to their mental status. A second article, by John Marshall<sup>21</sup>, another friend of Huxley's, made essentially the same points about the chimpanzee. Presumably to establish his credibility, Marshall denied 'leaning toward any of the developmental hypothesis of the origin of species'.

Owen answered Huxley and his allies in lectures and journals, continuing to insist stubbornly on his claims of the three structures unique to man, but hedging a little by admitting that apes do not have a hippocampus minor 'as defined in human anatomy'<sup>13,22</sup>.

Soon Huxley produced his own anatomical study on the spider monkey<sup>10</sup>. Again, the emphasis was on refuting Owen's three points, particularly on the hippocampus minor. In the course of his detailed study of this structure, Huxley corrected a major error in previous descriptions of primate brains and effected a lasting change in sulcal terminology. Before Huxley, the major sulcus on the medial surface of the hemisphere was termed the hippocampal fissure and was supposed to extend from the corpus callosum to almost the posterior pole. While studying sections through the hippocampus minor, Huxley realized that this hippocampal fissure consisted of two separate sulci, a posterior and anterior one. The indentation of the posterior one into the lateral ventricle formed the hippocampus minor, so he named it the calcarine sulcus after *calcar avis*, the original term for the hippocampus minor. He named the anterior part the dentate sulcus. 'Calcarine sulcus' entered into the permanent canon but the term hippocampal fissure was maintained for the anterior part (except by Huxley's followers).

The Gov. School of Mines  
 Jermyn St. August 4 1862

Before making my report upon  
 Mr Flower's paper on the posterior  
 lobe of the cerebrum in the *Quadrumanus*  
 it is right that I should state  
 that the questions therein  
 discussed have been the subjects  
 of controversy: that I have taken  
 an active part in that  
 controversy: & that Mr Flower's  
 memoir contains a complete  
 confirmation of the statements  
 I have made

This much being premised  
 in order that the Committee of  
 Papers may form their own  
 judgment as to the extent  
 to which my opinion is likely  
 to be prejudiced, I may  
 say, that both as regards  
 manner & matter, Mr Flower's  
 memoir appears to me to be  
 eminently worthy of a place  
 in the *Philosophical Transactions*

• • •

Thomas H. Huxley

Fig. 2. The beginning of Huxley's referee report on Flower's paper submitted to *Philos. Trans. R. Soc.*<sup>23</sup> that took Huxley's side in the hippocampus minor controversy. The entire report (RR 4.97, Royal Society archives) is as follows:

'The Gov. School of Mines, Jermyn St. August 4, 1862. Before making my report upon Mr Flower's paper "On the posterior lobe of the cerebrum in the *Quadrumanus*" it is right that I should state that the questions therein discussed have been the subjects of controversy: that I have taken an active part in that controversy: & that Mr Flower's memoir contains a complete confirmation of the statements I have made. This much being premised in order that the Committee of Papers may form their own judgement as to the extent to which my opinion is likely to be prejudiced, I may say, that both as regards manner and matter, Mr Flower's memoir appears to me to be eminently worthy of a place in the *Philosophical Transactions*.

Wisely avoiding even the appearance of entering into controversial discussions Mr Flower has detailed with much clearness & precision of expression, a number of careful dissections – most of which have been made upon animals, whose brains we possess, at present, no sufficient account.

The results of Mr Flower's dissections of the Lemurine brains more particularly, are quite new & of very great importance.

If it can be done without inconvenience I should recommend that in the plates all the brains be drawn to the same absolute length – as the variation in proportions become in this way far more obvious –

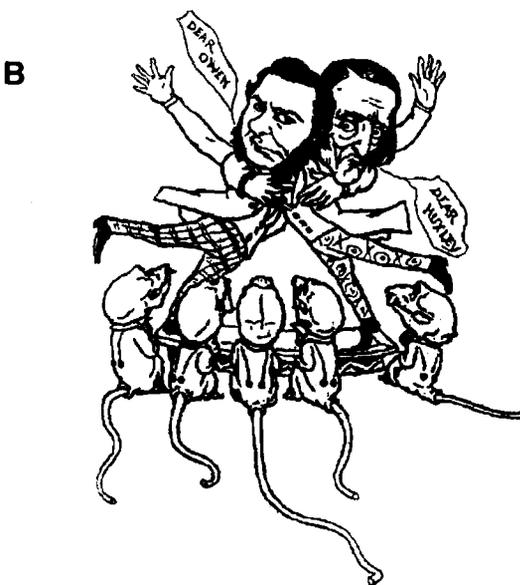
Furthermore, as M. Gratiolet has already maintained the view that the Lemurs form a distinct subspecies – a reference should be added to this effect – to that part of Mr Flower's paper which deals with this question. Thomas H. Huxley.'

The onslaught against Owen spread to that most prestigious venue of them all, *The Philosophical Transactions of the Royal Society*. There, another protégé of Huxley's, William Henry Flower, after stating that he had no views on the origin of man, proceeded to refute Owen's three man-ape distinctions on the basis of his own new dissections of 16 different primate species from prosimian to ape<sup>23</sup>. In addition to his being a friend of Flower's, Huxley's hand in the paper is shown in the nomenclature used and in that he was one of the anonymous

reviewers for the paper (Fig. 2). (The other reviewer was John Marshall, a member of Huxley's anti-Owen team of neuroanatomists.)

It probably was Huxley's *Evidence as to Man's Place in Nature*<sup>24</sup> that played a major role in finally defeating Owen. It derived from his lectures for working men at the School of Mines and sold widely. It contained travelers' anecdotes about the mental powers of apes as well as a review of the fossil evidence, but its core was the anatomical similarity of man and the apes, particularly their

**Fig. 3. (Right)** Examples of the popular reaction to the debate between Huxley and Owen on the hippocampus minor. **(A)** Drawing by Linley Sambourne of Owen (left) and Huxley examining a water baby, from a 1916 edition of Kingsley's novel *Water Babies*. **(B)** Owen and Huxley dancing a jig before the 1865 British Association meeting from *Punch*, Sept. 23, 1865, p. 113. **(C)** Title page of an eight-page squib anonymously published (and written by G. Pycroft). In it Owen and Huxley are dragged into court for brawling in the streets and disturbing the peace. The fight continues in court with much shouting of 'posterior cornu', 'hippocampus' and such. At the end of the trial, the Lord Mayor declined to punish either because 'no punishment could reform offenders so incorrigible'. He did suggest to Owen that, rather than being bitter about being compared to an ape, he might act less like one and more like a man. He suggested to Huxley that he was less interested in the truth than in destroying his rival.



**C**

**A Report**

or

**A SAD CASE,**

Recently tried before the Lord Mayor,

**OWEN versus HUXLEY,**

In which will be found fully given the  
Merits of the great *Recent*

**BONE CASE**

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LONDON,  
1863.

brains, with a six-page account of how Owen 'suppressed' and denied the truth about the hippocampus minor and how this was now a matter of 'personal veracity'. On the basis of this account, Sir Charles Lyell, one of Britain's most eminent scientists and no Darwinian (yet) came down totally and unambiguously on Huxley's side, effectively ending the debate in the scientific community<sup>25</sup>.

Owen's final statement on the hippocampus minor controversy is in his *On the Anatomy of Vertebrates*<sup>26</sup>. There he finally admits that in apes 'all the homologous parts of the human cerebral organ exist'. However, this does not invalidate his classification of man in a separate subclass because the critical structures; the posterior lobe, the posterior horn and the hippocampus minor, exist in apes only '... under modified form and low grades of development'. As to Huxley and his neuro-anatomical allies, their attacks on his classificatory scheme were 'puerile', 'ridiculous' and 'disgraceful'.

### The public laughs

Meanwhile, the popular press was having fun with cartoons and satires on the debate (see Fig. 3). A poem in *Punch* included these stanzas<sup>27</sup>:

Then HUXLEY and OWEN,  
With rivalry glowing,  
With pen and ink rush to the scratch;  
'Tis Brain versus Brain,  
Till one of them's slain;  
By Jove! it will be a good match!

Says OWEN, you can see  
The brain of a Chimpanzee  
Is always exceedingly small.  
With the hindermost "horn"  
Of extremity shorn,  
And no "Hippocampus" at all.

Next HUXLEY replies,  
That OWEN he lies,  
And garbles his Latin quotation;  
That his facts are not new,  
His mistakes are not few,  
Detrimental to his reputation

(These stanzas were anonymously signed 'Gorilla' and written by Sir Philip Egerton, a paleontologist and MP.)

Both Owen and Huxley were featured in Charles Kingsley's children's fantasy *Water Babies*, originally

## Acknowledgements

The author thanks M. S. A. Graziano, G. Krauthamer, H. R. Rodman, M. Sampson, L. R. Squire and R. M. Young for their help. Figs 1, 3A and 3B are courtesy of Princeton University Library; Figs 2 and 3C are courtesy of the Royal Society Archives.

published in 1863. At one point its child protagonist is puzzled at the strange things that are said at British Association meetings. He had thought that the difference between him and an ape was such things as 'being able to speak, and make machines, and know right from wrong, and say your prayers'... rather than having... 'a hippopotamus major in your brain'. He understands that... 'if a hippopotamus major is ever discovered in one single ape's brain, nothing will save your great-great-great-great-great-great-great-great-great-greater-greatest-grandmother from having been an ape too'.

## The demise of the hippocampus minor

By the 1890s the general idea of evolution, including of man, was accepted by the scientific community. The Rt Hon. Huxley was now at the very center of the new professional scientific establishment<sup>8,18</sup> and the new edition (1894) of *Man's Place in Nature* did not even mention the Owen controversy. Owen himself had died and in the ultimate confirmation of the saying 'history is written by the victors' when Owen's grandson wrote Owen's biography, he invited Huxley to write the portion on Owen's 'Position in the History of Anatomical Science'<sup>7</sup>. The term hippocampus minor soon disappeared; it had served its purpose in helping to establish Darwinism and replace the Oxbridge clergy-naturalist's control of science. The synonym 'calcar avis' returned, but only in obscure corners of human anatomy texts where it still rests.

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# letters to the editor

## Receptor-independent activation of mast cells by bradykinin and related peptides

In their recent *TINS* review article (March 1993), 'Bradykinin and inflammatory pain', Dray and Perkins reported that the actions of bradykinin (BK) on a variety of tissues and cells, including mast cells, occur through B<sub>2</sub> receptors. However, the existence of specific receptors for BK, BK-related kinins and other kinins on mast cells has been the subject of debate<sup>1,2</sup>.

We have demonstrated that secretory processes elicited by BK, substance P and mastoparan were decreased by pretreatment of mast cells with neuraminidase<sup>3,4</sup>, indicating that sialic acid residues of the cell surface are involved in the initial binding of these peptides. The activation of

mast cells by amphiphilic peptides involves a G protein sensitive to pertussis toxin, and phospholipase C activation (reviewed in Ref. 5). We and others have proposed that direct activation of a G protein is the physiological mechanism of action for cationic amphiphilic peptides on mast cells<sup>5–8</sup>. The peptide-interacting site of the G protein has been shown to be at the C-terminus of the  $\alpha$  subunit<sup>9,10</sup>. This pathway of mast-cell activation was also proposed for BK<sup>4,5,11</sup>. Bradykinin induced a transient increase in inositol 1,4,5-trisphosphate and Ca<sup>2+</sup> mobilization, which was inhibited by pertussis toxin. Bradykinin and related peptides, including BK antagonists, also stimulate the GTPase activity of purified G proteins<sup>4</sup>. Binding assays on rat peritoneal mast cells have been unable to provide evidence for membrane receptors specific for BK; only nonspecific

binding of [<sup>3</sup>H]BK has been observed (J.P.G., Y.L., M.M., unpublished observations). The potency order of kinins on histamine release from mast cells has been related to the number of positively charged amino acid residues, and the current B<sub>1</sub>- and B<sub>2</sub>-receptor antagonists also induce histamine release<sup>12</sup>. The linear correlation between the histamine-releasing potencies and the density of positively charged amino acid residues of amphiphilic peptides has also been demonstrated in the case of anaphylatoxin C3a and C3a synthetic peptides<sup>13</sup>. Finally, there is no clear evidence to suggest that the activation of mast cells is via B<sub>2</sub> receptors. A process that is receptor-independent but membrane-assisted remains the only documented mechanism of action for cationic amphiphilic peptides including BK, in mast cell activation.