

TABLE 1 Responses of birds to butterflies

Bird	Number entirely eaten				Percentage entirely eaten				Mean response score				Mean manipulation time			
	C	Q	V	M	C	Q	V	M	C	Q	V	M	C	Q	V	M
A	22	0	1	0	92	0	12	0	2.92	0.50	0.88	1.25	5.2	—	—	—
B	24	6	5	5	100	75	62	62	3.00	2.62	2.25	2.50	5.3	18.9	12.4	25.9
C	24	5	5	4	100	62	62	50	3.00	2.44	2.50	2.12	8.2	25.2	26.6	19.6
D	24	7	4	5	100	88	50	62	3.00	2.88	2.12	2.25	3.1	12.4	41.6	27.4
E	24	5	0	4	100	62	0	50	3.00	2.69	1.06	2.38	8.6	36.5	—	58.5
F	24	7	2	2	100	88	25	25	3.00	2.75	1.62	1.38	8.7	16.4	47.0	25.0
G	23	5	3	3	96	62	38	38	2.96	2.50	1.94	1.94	4.5	18.1	24.2	30.0
H	24	6	5	3	100	75	62	38	3.00	2.62	2.62	2.19	3.8	10.0	35.3	32.1
I	24	6	8	1	100	75	100	12	3.00	2.75	3.00	1.62	3.9	11.4	13.2	49.4
J	24	6	2	8	100	75	25	100	3.00	2.69	1.69	3.00	3.2	13.5	22.1	15.2
K	24	8	2	5	100	100	25	62	3.00	3.00	1.81	2.38	3.4	16.5	15.4	18.7
L	22	4	2	2	92	50	25	25	2.92	2.00	1.88	1.25	4.7	21.0	20.8	30.0
M	23	4	4	3	96	50	50	38	2.92	2.50	2.50	2.38	9.1	25.4	23.9	39.1
N	24	8	4	8	100	100	50	100	3.00	3.00	2.00	3.00	4.6	7.6	7.5	23.7
O	24	4	6	2	100	50	75	25	3.00	2.50	2.38	2.00	5.2	15.7	15.0	42.6
P	23	6	0	4	96	75	0	50	2.92	2.50	1.38	2.00	7.0	13.6	—	32.6
\bar{x}	23.6	5.4	3.3	3.7	98	68	41	46	2.98	2.50	1.98	2.10	5.3	17.5	23.5	31.3
s.e.	0.2	0.5	0.6	0.6	1	6	7	7	0.02	0.15	0.14	0.13	0.5	1.9	3.3	3.0

Individual responses of 16 red-winged blackbirds to control (C), queen (Q), viceroy (V) and monarch (M) abdomens. Means are compared statistically in Fig. 1. Response score described in Fig. 1; manipulation time is in seconds (birds eating no abdomens of a given species have no manipulation time recorded). Individual birds differed in their treatment of viceroys and danaines; this is an important aspect of mimicry dynamics.

contrast, the viceroy/queen relationship is asymmetrical, with the viceroy a stronger (more unpalatable) co-model than the queen. Mathematical models of müllerian mimicry suggest that the queen actually benefits more from the mimicry than does the viceroy²³, perhaps even at the viceroy's expense²⁴, reversing the traditionally accepted roles of model and mimic.

Our laboratory study shows reactions of one predator species to abdomens from representative Florida populations; extrapolating to natural interactions involving multiple predators and variably palatable butterflies must obviously be done with caution. Nonetheless, our finding of müllerian mimicry prompts a reinterpretation of viceroy-danaine-predator interactions. The classic batesian interpretation of viceroy-danaine mimicry predicts that only the viceroy benefits, at the expense of both danaines (which it 'parasitizes') and predator (which it deceives into eschewing palatable prey). By contrast, the new müllerian interpretation predicts that all three species benefit from enhanced predator learning, which occurs because of the viceroy and danaine co-models' shared aposematic signal. Our findings therefore imply that the butterflies and their predators interact in a selective milieu very different from that previously assumed, and suggest that other 'classic' mimicry relationships warrant closer scrutiny.

Further investigation of viceroy mimicry will not only clarify the nature of this particular system, but will also potentially give insights into the dynamic processes of selective predation that shape mimicry relationships in general. The viceroy-danaine system offers an opportunity to test mathematical and conceptual models^{6,23} of dynamic müllerian mimicry, and provides an interesting comparison to previous studies of müllerian mimicry in which the co-mimics are more closely related (for example, *Heliconius* butterflies²⁵ or *Zygaena* moths²⁶). Thus, over a century after its discovery, the viceroy-danaine relationship continues to contribute to our understanding of the evolution and ecology of mimicry. □

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Left neglect for near but not far space in man

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IT has been suggested that, among the many visual areas of the human brain, there might be one set of spatial maps specialized for 'near' (peripersonal) and another for 'far' (extrapersonal) space. A distinction between 'grasping distance' and 'walking distance'¹, or between a 'reaching field' and a 'pointing or throwing field'² has commonly been made. Evidence for such a division has been found in monkeys. Unilateral ablation of the frontal eye field (area 8) produces a more prominent inattention (or 'neglect') for objects in contralesional far space than in near space; by contrast, unilateral ablation of frontal area 6, which receives direct projections from area 7b (the rostral part of the inferior parietal lobules) results in inattention to visual stimuli limited to contralesional near space³. Despite predictions that comparable dissociations should be found in man⁴, there has been no convincing evidence. We report here such evidence in a patient with a unilateral right hemisphere stroke. Within peripersonal space, he showed severe left visuo-spatial neglect on conventional tests, including the highly

TABLE 1 Transection displacements in millimetres from true centre

Step		1 Near space (pen)	2 Far space (light pen)	3 Far space (darts)	4 Near space (pen)	5 Near space (light pen)
Line length (cm)						
Near	Far	Mean (s.d.)	Mean (s.d.)	Mean (s.d.)	Mean (s.d.)	Mean (s.d.)
30.5	166	+46.3 (24.8)	-4.3 (3.8)	+22.5 (4.8)	+64.3 (22.7)	+38.3 (9.7)
25.4	138	+64.7 (18.9)	+12.5 (15.5)	+11.7 (4.7)	+43.2 (19.9)	+27.3 (19.3)
20.3	114	+37.0 (12.1)	-10.0 (4.2)	+19.0 (4.3)	+33.0 (6.5)	+29.9 (9.7)
15.2	83	+26.5 (6.7)	-2.3 (4.9)	+1.0 (6.5)	+27.7 (10.1)	+12.8 (7.5)
10.2	56	+18.7 (8.9)	-3.3 (3.4)	+0.8 (3.9)	+24.3 (5.5)	-0.3 (8.2)
5.1	27	+4.8 (2.7)	-5.4 (3.2)	-3.8 (4.5)	+2.8 (1.7)	-6.1 (6.9)

Line bisection performance in the five experimental conditions: step 1, displacement from true centre at viewing distance 450 mm (bisection with a pen); step 2, displacement at viewing distance 2.44 m (bisection with a light-pen); step 3, displacement at viewing distance 2.44 m (bisection by dart-throwing); step 4, repetition of step 1; step 5, displacement at viewing distance 450 mm (bisection with a light-pen, six weeks later). The best-fitting linear equations for transection displacement as a function of line length (expressed as visual angle) are: 1, $-3.46 \text{ mm} + (1.630 \times \text{visual angle})$ (81%); 2, $-6.57 \text{ mm} + (0.198 \times \text{visual angle})$ (9%); 3, $-10.25 \text{ mm} + (0.840 \times \text{visual angle})$ (83%); 4, $-5.09 \text{ mm} + (1.683 \times \text{visual angle})$ (92%); 5, $-16.15 \text{ mm} + (1.481 \times \text{visual angle})$ (95%). The final figures in brackets are the percentages of variance captured.

sensitive task of line bisection. When line bisection was performed in extrapersonal space, neglect was abolished or attenuated.

T.M. is a 57-year-old, right-handed mechanic who suffered a right hemisphere stroke on 1 July 1990. On admission (3 October 1990), T.M. had a severe left hemiparesis and a left inferior homonymous quadrantanopia; there was a full range of ocular movements and visual acuity was 6/9 in both eyes. Magnetic resonance imaging of the brain (29 November 1990) showed a large area of abnormality in the right hemisphere, with no signs of left hemisphere damage. Within the territory of the middle cerebral artery, his posterior parietal cortex is infarcted with some sparing of superior and medial parietal cortex (but the latter is undercut by deep white matter lesions). Most of the lateral and medial temporal cortex is affected, with dilation of the right temporal horn. There is also damage to the right cerebral peduncle, pons and internal capsule. The frontal pole and frontal cortex are spared, although the lateral inferior aspect of the right frontal lobe is affected. The occipital cortex is intact (hence the quadrantanopia is due to a tract lesion). Consistent with an intact left hemisphere, T.M. had a verbal intelligence quotient (109) that was within normal limits.

The outstanding neuropsychological symptom was left visuo-spatial neglect. Assessed on the Behavioural Inattention Test⁵, T.M. scored 71/146. This aggregate is derived from performance on: line- (23/36), letter- (17/40), and star-cancellation (29/54); line bisection (0/9); figure copying (0/4); and representational drawing to verbal request (2/3). The cut-off for normality is 130/146. On another line bisection task, where 11 horizontal lines between 25 mm and 279 mm are each presented 10 times in random order for bisection, T.M. performed very poorly. The mean of his transections was displaced rightwards at all line lengths; the linear regression of transection displacement on line length was $-6.23 \text{ mm} + (0.3194 \times \text{line length})$, and accounted for 99% of the variance. The multiplier (+0.3194) is over an order of magnitude larger than that in any member of a sample of 20 normal control subjects⁶. T.M. thus manifested classical left visuo-spatial neglect within peripersonal space. He did not show personal neglect. On verbal command, T.M. could touch left-sided parts of his body (elbow, shoulder, wrist, ear, thumb, knee, calf and thigh) with his right hand. Performance was without error, both with eyes open and eyes closed. The observations that follow were made during one testing session, 20 weeks after the stroke. Because of his hemiplegia, T.M. remained in his wheelchair throughout the session. Normal room illumination was maintained.

The investigations were conducted in the following order. Step 1: Black horizontal lines (2 mm thick) were individually drawn on sheets of paper (297 × 420 mm). Six line lengths were used; 51, 102, 152, 203, 254 and 305 mm. Each line, presented on a separate sheet, was centred on the page both horizontally

and vertically. The midpoint of each sheet was positioned at eye-level on a vertically oriented board directly in front of the patient. Viewing distance was ~450 mm, well within peripersonal space, and the visual angles subtended by the stimuli accordingly ranged between 6.4° (51-mm line) and 37.6° (305-mm line). The patient was instructed to mark the midpoint of each line with a fine pen held in the right hand. Step 2: A vertically oriented white board, 1.83 m long by 0.61 m high, was positioned so that the centre of the board was at eye-level for the patient in the wheelchair. Horizontal black lines (20 mm thick) were individually displayed on the board, centred both horizontally and vertically; the lines were lengths of PVC (polyvinylchloride) tape that could be easily attached to (or detached from) the surface of the board. Six line lengths were used: 27, 56, 83, 114, 138 and 166 cm. The patient was positioned 2.44 m from the board, so that the centre of each line fell on his midsagittal plane. Viewing distance is far outside peripersonal space and the visual angles subtended by the line stimuli are roughly the same as those used in step 1. The patient now bisected these lines with a lightweight theatre pointing-light held in the right hand. This pointer projected a thin v-shape cleanly on the screen. T.M. was asked to make a single movement to the centre of the line and then indicate his judgment by depressing a small button on the top of the pointer, thereby producing the illuminated v. Step 3: The apparatus was the same as that used in step 2. The patient (a keen darts player) was now requested to mark the midpoint of each line by throwing a dart from a distance of 2.44 m, which is the normal throwing distance for the game. Step 4: This stage is the same in all respects as step 1. It is a control for any effects of experience or 'learning'. For each step, six trials per line length were given in pseudo-random order, and the horizontal displacement of T.M.'s transections from true centre was measured to the nearest millimetre.

Mean displacements (+ for rightwards, - for leftwards) and standard deviations for each condition are shown in Table 1. Statistical comparisons (paired *t*-test) are based upon absolute (signed) displacements. There is no significant difference between conditions 1 and 4 ($t = 0.085$, degrees of freedom (d.f.) = 5), and hence no 'learning' effect across the experimental session. By contrast, the difference between the results of conditions 1 and 2 is significant ($t = 4.9$, d.f. = 5, $P < 0.01$). Likewise, the other far-space condition (step 3), yields a data set that is significantly more accurate than was found in near space in step 1 ($t = -3.95$, d.f. = 5, $P < 0.01$).

Two final controls were run in separate sessions. Some patients with neglect can bisect rectangles and squares with greater accuracy than lines. In the preceding experiment, the vertical visual angle subtended by the lines in far space was almost double that of the lines in near space. Accordingly, we replicated

steps 1 and 4 with lines of the same length but now 4 mm thick. The results did not differ significantly from those obtained with lines 2 mm thick; variation in the vertical visual angle of the stimuli is therefore not responsible for the observed differences in performance in near and far space. Six weeks after the main experiment we also replicated steps 1 and 4 in a condition where T.M. bisected each line six times in near space with a pointing light held immediately in front of the body (step 5). An analysis of variance with repeated measures, found no significant difference ($f = 8.01$, d.o.f. = 5, 2) between conditions 1, 4 and 5. The differences between performance in near and far space are therefore not due to the response-mode *per se*. There is a significant difference between conditions 2 and 5 ($t = -2.56$, d.o.f. = 5, $P < 0.02$), both of which employ a light-pen.

The data thus show that severe left visual neglect in peripersonal space can coexist with minimal or no neglect in extrapersonal space. Previous failures to discover this dissociation⁷ may indicate the rarity of isolated peripersonal neglect; most patients with persistent left visual neglect have large lesions in the territory of the right middle cerebral artery that may "disrupt more than a single neural system"⁷. Alternatively, these failures may reflect an inadequate choice of experimental task (for example, tests of purely perceptual judgment)⁷. Our extrapersonal tasks require explicit visuo-motor skills that might be expected to map onto an extrapersonal spatial field dedicated to pointing and throwing functions². In future work, it would be pertinent to investigate the pattern of eye movements to near and distant objects; subjects may scan a display differently according to its perceived distance from the viewer.

Previc has recently suggested⁸ that "functional differences between near and far visual space are correlated with their disproportionate representations in the dorsal and ventral divisions of visual association cortex, respectively, and in the magnocellular and parvocellular pathways that project to them."⁸ Our results corroborate the functional distinction, although the extent of T.M.'s lesion is not compatible with the emphasis placed on the role of temporal cortex in attending to far space^{4,8}. The relative preservation of frontal cortex (area 8 in particular) may thus be responsible for T.M.'s accurate performance in extrapersonal space⁹. This extrapolation from studies in monkeys could, however, be questioned.

Some studies of monkey show clear contralateral visual neglect for near space after removal of area 8 (refs 10, 11). When Rizzolatti *et al.*³ reported more severe neglect in far than in near space after ablation of area 8, the stimulus may have been less prominent in far space; the stimuli to which the animals responded may have subtended a much greater visual angle when they were close to the head.

Our behavioural findings extend previous reports of dissociations between personal neglect (in the sense of failure to point on command to a part of one's own body) and failure to explore adequately visual arrays presented within arm's reach¹². Personal neglect (not shown by T.M.) is much less frequent than is neglect of external visual stimuli¹². Above all, the distinction seen in T.M. between reaching and pointing or throwing in far space confirms the teleology of action stressed by Brouchon *et al.*²: "... the ultimate intention of action can determine not only the elaboration and the execution of the movement but also, at least in part, the processing of the perceptual cues associated to the movement." □

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Requirement for nerve growth factor in the development of myelinated nociceptors *in vivo*

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IN adult animals, sensory neurons innervating the skin are phenotypically diverse¹⁻³. We have now investigated whether nerve growth factor (NGF) has a physiological role in the development of this diversity. We gave antisera against NGF to rats from postnatal day 1 (PND 1) to adulthood (5 weeks). We found a virtually complete depletion of high threshold mechanoreceptors conducting in the A δ range (2-13 m s⁻¹) in the sural nerve. This afferent type, normally present in large numbers, appeared to have been replaced by D-hair afferents, sensitive mechanoreceptors which normally are relatively rare. NGF deprivation had this effect only in early postnatal life; treatment from postnatal day 14 to adulthood had no effect. We conclude that the presence of NGF postnatally in skin is necessary for the proper phenotypic development of A δ cutaneous nociceptors.

Rats (Sprague-Dawley) were treated from birth for 5 weeks with antisera against mouse 2.5S NGF (anti-NGF). In the terminal experiments, extracellular single unit recordings were made from 123 A δ (2-13 m s⁻¹) and 175 A β afferents (>13 m s⁻¹) (Fig. 1a). The physiological properties of A β fibres, such as receptive field size, threshold, modality and conduction velocity, were indistinguishable from those of units in control animals.

By contrast, the population of A δ fibres was radically altered. In controls, the largest proportion (45%) consisted of cutaneous high threshold mechanoreceptors (HTMRs), which encode noxious mechanical events (Fig. 1a) which can lead to pain^{2,4-6}. Low threshold hair afferents, D-hairs^{1,5}, constituted a smaller percentage of the total (26%), and the remaining A δ afferents (29%, see Table 1) were usually high threshold but innervated subcutaneous tissue ('deep'). In animals treated from birth with anti-NGF, cutaneous HTMRs all but disappeared (5-7% of the total), and most (64-72%) of the cutaneous A δ fibres innervated D-hairs (see Table 1). But deep afferents were similar to those in controls both in relative frequency (Fig. 2; Table 1) and in adequate stimulus.

TABLE 1 Physiology of A δ fibres

	Control	Anti-NGF 2-5 weeks	Anti-NGF 0-5 weeks	Anti-NGF +recovery
HTMR	14 (45%)	15 (38%)	1 (5%)	2 (7%)
D-Hair	8 (26%)	12 (31%)	16 (72%)	20 (64%)
Deep	9 (29%)	12 (31%)	5 (23%)	9 (29%)
Total	31 (n=8)	39 (n=3)	22 (n=5)	31 (n=3)

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