Delay argument. The assumption is that, since perception of pain is delayed, a different set of neurons, with slower conduction times, is required. There is good evidence for a progressively increasing latency of action potentials in blocked nerves. Clark, Hughes, and Gasser (*9*) found slight slowing of conduction rates apparent within 15 minutes. Records of action potentials in the human ulnar nerve show progressive increase in latency after inflation of the pressure cuff (*10*). There was no discontinuity in the curve as would be expected if the composition of the group of active neurons had changed. Similar delays in perception occur in the other cutaneous senses also (*6, 7*). I would assume the perceptual delay to be due to the increasing latency of action potentials in neurons subjected to pathological conditions, and possibly also to synaptic delays occasioned by reduction in number of afferent impulses reaching the central nervous system.

Reliability of ischemia-nerve block data. The assumption is that such data are reliable and give reliable indices of conduction times of fibers. It is clear that the results of such experiments on human subjects are variable. If a large number of subjects is used and if the results are treated statistically (*6, 7*), the order of loss is seldom significant. Landau and Bishop themselves (*4*) found procaine blocks to be "inconclusive" because prick and deep pain disappeared together—that is, because the sensory results did not bear out the results of action-potential studies. Whereas touch may usually fail before pain in compression of a limb, the difference is not sufficiently dramatic to enable one to distinguish between small delta fibers and C fibers. There is evidence that the survival time of fibers under compression block is influenced by factors other than conduction rates. Frankenhauser (*11*), who dealt with touch fibers of different types, found that slowly adapting touch receptors in the rabbit were blocked later than hair touch fibers in spite of the fact that their conduction rates completely overlap those of the latter. He concluded that the fibers themselves have properties which are not predictable from observation of the impulses. In man, skin touch and hair touch also have different survival times (*12*), and in some areas hair touch survives pain (*6*).

There are some interesting results which suggest that the somatic sensory apparatus is much more complex than the current popular notions would have it. Between giving up all specificity, as Sinclair (*13*) does, and being bound to one or even two specific pain modalities, as Bishop and Landau are, one can conceive a rich patterning of general somatic sensation, with a large number of different sorts of receptors having different functions and different response characteristics. Maruhashi, Mizuguchi, and Tasaki (*14*) found a great variety of types of afferent nerve fibers in the toad and cat. These varied not only in fiber size, but in type of discharge (tonic or phasic), size of receptive field, and type of stimulus most effective. I would assume that a given stimulus excites more than one kind of fiber; thus the perceptual pattern is normally a complex one, not only spatially and temporally, but also in the balance of fiber types activated. And a different stimulus, since it affects a dynamic organism, will have a different effect.

My conclusions are as follows. (i) The exact function of the C-fibers is not known. These fibers respond to noxious stimuli but whether this results in awareness or merely feeds into either the reticular activating system or into an "affect" system is not certain. (ii) The peculiar quality and delay of pain sensations in nerve-block experiments are probably due to pathologically functioning tissues. (iii) Somatic sensation is a vastly complex system. (iv) Second pain is certainly an artifact in normal human experience.

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Tolerance to Cereal Leaf Rusts

Resistance of crop varieties to plant rust fungi has been attained thus far mainly through utilization of the hypersensitive reaction wherein the host and parasite are mutually incompatible, resulting in localized necrosis of host tissue and in death or limited growth of the parasite. Such hypersensitivity, hereafter referred to as resistance, has afforded excellent initial rust protection to new resistant varieties produced by plant breeders. However, when such resistant cereal varieties have been extensively grown, new virulent varients (physiologic races) of the rust fungi have consistantly arisen to render these varieties fully susceptible in nature. Three genetically distinct hypersensitive types of resistance to the crown-rust fungus, *Puccinia coronata* Cda., have been transferred to extensively grown, commercial oat varieties in the United States. All such varieties, although providing high resistance to the initially occurring populations of the pathogen, have succumbed to attack by new physiologic races within a few years after they have been extensively grown. A similar fate has befallen oat and wheat varieties once resistant to prevalent races of stem rust, *Puccinia graminis* Pers. These experiences direct attention to the need for plant characters, other than resistance, whereby rust damage may be prevented or reduced.

Tolerance, enabling a susceptible plant to endure severe attack by a rust fungus without sustaining severe losses in yield or quality, is such a character. Caldwell *et al.* (*1*) have shown that the yield of Fulhard wheat in Indiana is not affected by severe attack of the leaf-rust fungus, *Puccinia recondita* Rob. ex. Desm. f. sp. *tritici.* This finding was supported by the report of Salmon and Laude (*2*) that the Fulhard variety was the highest yielding of 24 varieties studied over a period of years in Kansas, although it was one of the most severely attacked by leaf rust.

Evidence that a high level of tolerance to the crown-rust fungus, *P. coronata,* exists in the Benton variety of oats was obtained in studies at Lafayette, Indiana, from 1955 to 1957. Two pairs of oat varieties were involved in these studies, each pair being nearly "isogenic" except that one member of each pair was highly resistant to crown rust while the other was highly susceptible. Pair No. 1 consisted of the varieties Clinton 59 and Clintland. They differed essentially by a genetic factor for resistance to crown rust which had been introduced into Clintland by a cross of Clinton 59 × Landhafer, followed by three backcrosses to Clinton 59. Pair No. 2 consisted of the varieties Benton and Bentland that also differed mainly by the same genetic factor for resistance which had been introduced into Bentland by a cross of Benton × Landhafer, followed by six backcrosses to Benton.

There is little difference between the members of these pairs of varieties in appearance or in yield and quality of grain, when grown in the absence of crown rust, as was shown by 16 replicated field-plot trials conducted in Indiana from 1954 to 1956 by Newman *et al.* (*3*). Crown rust was absent in 15 of these trials and occurred as only a trace in one. The mean yields and bushel weights of the two pairs of varieties for this period, obtained under crown-rust-

Table 1. Comparative grain yields of crown rust susceptible (nontolerant), susceptible (tolerant), and resistant oat varieties. Reactions to crown rust: Clinton 59, susceptible, nontolerant; Clintland, resistant; Benton, susceptible, tolerant; Bentland, resistant.

Variety	Crown rust free (Av. yield 1954–56*)		Exposed to severe crown-rust attack					
			1955		1956		1957	
	bu/acre	Diff. (%)	bu/acre	Diff. (%)	bu/acre	Diff. (%)	bu/acre	Diff. (%)
			"Isogenic" pair No. 1					
Clinton 59	69.3	− 3.9	109.1	− 20.7	86.8	− 28.6	43.3	− 54.0
Clintland	72.1		137.5		121.6		94.2	
			"Isogenic" pair No. 2					
Benton	64.3	+ 1.4	91.9	+ 5.4	100.5	− 6.5	74.0	− 13.8
Bentland	63.4		87.2		107.5		85.8	
L.S.D. (5%)	2.1		21.4		10.1		16.6	

* Average of 16 replicated tests.

Table 2. Comparative test weights of crown rust susceptible (nontolerant), susceptible (tolerant), and resistant oat varieties. Reactions to crown rust: Clinton 59, susceptible, nontolerant; Clintland, resistant; Benton, susceptible, tolerant; Bentland, resistant.

Variety	Crown rust free Av. 1954–56*		Exposed to severe crown-rust attack					
			1955		1956		1957	
	lb/bu	Diff. (%)	lb/bu	Diff. (%)	lb/bu	Diff. (%)	lb/bu	Diff. (%)
			"Isogenic" pair No. 1					
Clinton 59	33.4	− 2.9	32.6	− 13.5	28.9	− 11.3	18.9	− 30.5
Clintland	34.4		37.7		32.6		27.2	
			"Isogenic" pair No. 2					
Benton	34.7	0.0	34.5	− 2.5	31.8	− 2.8	21.8	− 21.9
Bentland	34.7		35.4		32.7		27.9	

* Average of 16 replicated tests.

free conditions, are presented in Tables 1 and 2 for comparison with their performance under crown-rust epidemics.

The same two pairs of varieties were exposed by us to severe, artificially induced, crown-rust epidemics in nursery-row performance trials in 1955, 1956, and 1957. The trials consisted of randomized, quadruplicate plots of each variety. Each plot consisted of four rows, 7.5 feet long, spaced 1 foot apart from which the center two rows were harvested for yield and bushel weight determinations. Mixed populations of physiologic races of crown rust that were highly virulent to Clinton 59 and Benton but avirulent to Clintland and Bentland were used in creating the crown-rust epidemics. The crown-rust infection reached 100 percent (maximum possible intensity) on the susceptible Benton and Clinton 59 in all three years, ultimately destroying all foliage, but in 1957 reached maximum proportions at an earlier stage of host development. In contrast, only a trace of crown rust developed on the resistant Bentland and Clintland.

Data on performance under rust attack are reported in Tables 1 and 2. In 1955 and 1956 the losses in yield, and in quality as measured by bushel weight, of the susceptible but tolerant variety Benton were nil or small as deduced from comparison with its resistant counterpart, Bentland. In contrast, the losses to the susceptible and nontolerant Clinton 59 were severe as deduced from comparison with its resistant counterpart, Clintland. Under the extremely severe epidemic of 1957 the same type of comparisons showed a yield loss of only 13.8 percent for Benton versus a 54.0 percent loss for Clinton 59. Likewise, the bushel weight of Benton was reduced 21.9 percent while that of Clinton 59 was reduced 30.5 percent.

Another measure of the tolerance of Benton is gained by direct comparison of its yield and quality with that of Clinton 59 (Tables 1 and 2). Both varieties appear to be completely susceptible to crown rust. Clinton 59 was significantly the higher yielding of the two in the absence of crown rust; yet under severe epidemics Benton gave much the higher yields in two out of the three years it was tested.

Since the crown-rust attacks on Benton and Clinton 59 appear to be equally massive, it is apparent that damage to functions and structures affecting yield and grain quality was much more severe in the variety Clinton 59 than in Benton. The losses of grain in Benton attributable to crown rust were not significant at the 5-percent level, while losses to Clinton 59 were significant. This performance would indicate a true tolerance of a high order in the susceptible variety Benton.

The tolerance exhibited by Benton should not be confused with intermediate degrees of rust resistance which have been erroneously referred to as tolerance despite the fact that they involve a degree of hypersensitivity. Varieties of such intermediate resistance, like those having more complete resistance, are also subject to "loss" of resistance in the presence of new races. This has been shown by experience with several oat varieties including Mo. 0-205 and Newton when subjected to race 216 of crown rust.

Theoretically, tolerance should be more stable than hypersensitivity-induced resistance. Should a physiologic race of the pathogen arise to which a previously tolerant variety would be nontolerant, the outcome would be a greater injury to the host with no consequent increase in the relative rate of proliferation of the newly arisen race as compared with that of the established races toward which tolerance is exhibited. This would provide no screening mechanism whereby the new race might gain an advantage over the established races and thereby replace them. This situation would be in marked contrast to the known competitive advantage gained by a new virulent race that can successfully parasitize a variety that is hypersensitive (resistant) to the prevalent races.

The heritability of tolerance to either oat crown rust or wheat leaf rust has not been investigated. Such studies have been initiated, and the possibility of introducing true tolerance into varieties of superior type, quality and yielding ability will be explored (*4*).

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