tachyzoites and bradyzoites to other intermediate hosts, and by noninfectivity of oocysts to nonimmune final hosts. While parasitism of skeletal muscle is a pronounced feature of the new genus *Hammondia*, it differs from *Sarcocystis*, the classical muscle parasite, by slender bradyzoites, thin-walled cysts, absent radial spines, septa, or metrocytes, by a multiplicative cycle in the gut of the final host (which is lacking in all *Sarcocystis* so far studied), and by shedding of unsporulated oocysts (whereas all known *Sarcocystis* shed sporulated sporocysts or oocysts).

The new genus differs from the common *Isospora* of cats, which are typically one-host parasites, with the oocyst infectious to the final host. However, an isosporan of dogs studied by Heydorn (*5*) is probably a species of *Hammondia*, since the oocysts were not infectious to dogs, whereas muscles of infected calves did infect dogs.

Hammondia hammondi is the first organism described which produces cross-reacting antibody to *Toxoplasma gondii* in the dye test. This could lead to a mistaken diagnosis of *Toxoplasma* infection in animals. It is not known whether humans become infected with *Hammondia*; however, morphologically compatible cysts have been observed by one of us (J.K.F.).

Recognition of an isolate of *Hammondia* could be delayed by misinterpreting the *Toxoplasma* antibody titer in the intermediate host. The isolate could be lost if tissue cysts were subinoculated from one to another intermediate host instead of to a final host which may be unknown. Prevention of the infection depends also on knowledge of the two-host cycle.

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References and Notes

1. J. P. Dubey and J. K. Frenkel, *J. Protozool.* **19**, 155 (1972); *J. Parasitol.* **59**, 505 (1973).
2. J. K. Fenkel, *Z. Parasitenkd.* **45**, 125 (1974); ______ and J. P. Dubey, *ibid.* **46**, 3 (1975).
3. N. D. Levine, in *The Coccidia: Eimeria, Isospora, Toxoplasma, and Related Genera*, D. M. Hammond and P. L. Long, Eds. (University Park Press, Baltimore, 1973), p. 1.
4. G. D. Wallace, *Science* **180**, 1375 (1973); *Z. Parasitenkd.*, in press.
5. A.-O. Heydorn, *Berl. Munch. Tierarztl. Wochenschr.* **86**, 323 (1973).
6. Supported by NIH grant AI-07489.

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Superior Colliculus: Visuotopic-Somatotopic Overlap

Abstract. *A laminar organization was present in the superior colliculus of the cat, with upper layer cells exclusively visual, lower layer cells primarily somatic (or acoustic), and intermediate layers showing significant modality overlap. The close topographic correspondence between the visual and somatic representations observed within this laminar pattern and the similarities in visual and somatic response specificity may be consistent with the hypothesis that the colliculus combines several sensory modalities to facilitate tracking of a given stimulus.*

The nature of the profound visual deficits appearing after superior colliculus destruction in the cat has led to suggestions that it is involved in visually guided (orienting and following) behavior (*1, 2*). Although relatively little is known about the properties of nonvisual cells in the superior colliculus, the colliculus is known to receive somatic and acoustic afferents in addition to visual projections (*3*). The developmental chronology of sensory representation in the cat superior colliculus has been shown to parallel the animal's use of modality-specific cues for tracking behavior (*4, 5*). Somatic stimuli are effective in activating superior colliculus cells at birth, when orientation is accomplished by means of somatic cues, while acoustic followed by visual activation develops many days later (*4*) along with auditory and visual orientation behavior. These observations, coupled with evidence that colliculus lesions induce somatic and auditory localization deficits (although less profound than visual consequences) (*1*), make it seem reasonable to suppose that just as the visual cells of the colliculus are involved in visual tracking behavior, somatic and acoustic cells are involved in somatic and auditory tracking behavior. In the present experiments we studied the location, organization, and specificity of tactile cells in the colliculus to determine whether the properties of these cells are consistent with this hypothesis. An abstract of this work has been presented (*6*).

Experiments were performed on 30 immobilized (*7*) and artificially respired cats. Animals were surgically prepared for recording with halothane anesthesia, and mixtures of 70 to 75 percent nitrous oxide and 25 to 30 percent oxygen were given during recording sessions. Visual receptive fields of superior colliculus cells were used as referents to which tactile receptive fields could be related. The pupils were dilated with 1 percent atropine, and the locations of the optic discs were determined with an ophthalmoscope and projected onto a transparent hemisphere used for mapping visual fields. Contact lenses focused the eyes on the hemisphere, and body temperature was maintained at 36 ± 2°C by a circulating hot water pad. When each experiment was terminated, intravenous pentobarbital sodium (40 mg per kilogram of body weight) was administered and the animal was perfused through the heart with saline followed by 10 percent formalin. The brain was sectioned at 15-μm thickness and stained with cresyl violet for histological reconstruction of electrode tracks.

Electrodes were vertically oriented. As an electrode was advanced through the laminae of the superior colliculus, natural visual, tactile, and acoustic stimuli (*8*) were delivered continuously. The upper layers of the colliculus proved to be exclusively visual (*9*); cells activated by tactile stimulation (N = 220) as well as acoustic cells were not encountered until the electrode reached the stratum griseum intermediale, where multimodal cells, which have been previously described (*10–12*), were also encountered. As the electrode advanced into the stratum profundum, the incidence of visually activated cells diminished markedly. A basic pattern emerged, with the upper layers strictly visual, the lower layers primarily nonvisual, and the intermediate layers representing a zone of "modality overlap."

Although tactile receptive fields ranged from a few millimeters in extent (primarily on the contralateral forepaw and face) to more than half the contralateral cutaneous surface, the organization was distinctly somatotopic. The presence of a well-ordered visuotopy in upper layer cells (*11, 13, 14*) enabled us to compare the spatial organization of the two modalities. This was accomplished by first mapping the contralateral visual fields of one to four single cells, or a multiunit group, in each of 85 electrode penetrations. The center of the group of receptive fields of each penetration was then used as the visual "reference point" to which the lower layer tactile receptive fields of that penetration were referred (Fig. 1).

In those penetrations in which the visual reference points were near the area centralis, tactile receptive fields were centered toward the midline of the face, near the nose. This is illustrated in the example of a reconstructed electrode penetration in Fig. 1. As the visual fields moved away from the area centralis, tactile fields also moved away from the nose in corresponding directions; for instance, penetrations in which visual reference points were immedi-

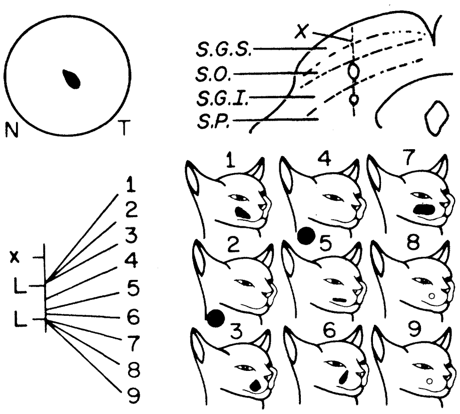

Fig. 1. Visual and somatic receptive fields in a single electrode penetration through the rostral portion of the left superior colliculus. The schematic drawing at upper right illustrates the penetration; *S.G.S.*, stratum griseum superficiale; *S.O.*, stratum opticum; *S.G.I.*, stratum griseum intermediale; *S.P.*, stratum profundum. At *X* a multiunit visual receptive field was mapped and its location is shown in the diagram of visual space at upper left; *T*, temporal; *N*, nasal. The somatic receptive fields of nine single units recorded within or below the stratum griseum intermediale, in this penetration, are illustrated in the figurine maps and numbered to correspond to positions along the needle track (lower left) indicating cell location, *L*, marking lesions. All the somatic cells except 2 and 4 [deep receptors in the neck (●)] were activated by low threshold tactile stimuli on the face. Receptive fields 8 and 9 were excited by the high velocity displacement of one or two vibrissae (○). In the 85 penetrations, a systematic relationship between upper layer visual and lower layer somatic receptive fields was observed. The parafoveal receptive fields of this penetration were represented above somatic receptive fields on the face.

ately superior to the area centralis were also those penetrations in which somatic receptive fields were located on the superior aspect of the head (crown). As the visual space sampled moved laterally (temporally), somatic fields moved laterally to the side of the head, neck, and shoulder. Visual reference points in ventrolateral (inferior temporal) space were in penetrations in which the forelimb was represented, and the most extreme portion of inferior temporal visual space that could be sampled corresponded to the forepaw (the forepaw can be viewed as the ventrolateral extreme of the body when the animal is standing or in a crouching position). The superior temporal area of visual space corresponded to hindlimb representation. Thus, the visuotopic-somatotopic relationship can be best viewed if the nose is pictured as superimposed on the area centralis and the limbs are seen radiating from this point at acute angles (Fig. 2).

There was a corresponding distortion of visual and body space in terms of the amount of superior colliculus tissue devoted to representing a given region. The disproportionately large area of colliculus devoted to the area centralis and parafoveal region (approximately the anterior half) and the inferior temporal visual space (approximately the posterolateral quarter) (*13*) constituted the area devoted to face, head, and forelimb. Thus, the somatic organization was not only discrete and topographic, but seemed to follow the design of the upper layer visual cells, which can also be conceived of as superimposed upon the lower layer cells representing the body (Fig. 2).

Presumably, the visuotopic organization of the superior colliculus is important for visual orienting and following behavior, with the magnified foveal representation in the colliculus providing for a zone of enhanced visual acuity. The parallel somatotopic organization, which also follows the distortion characteristics of the visuotopy, is consistent with a functional parallel. The magnified representation and small receptive fields of neurons representing the face and forelimb maximize tactile resolution in those zones of the skin employed for exploration, and for seizing and manipulating prey.

A number of specific visual response properties have been described as characteristic of superior colliculus cells. These properties indicate that these cells represent a select population and distinguish them from cells of the geniculocortical system. Activation is induced best, or only, by moving visual stimuli in superior colliculus cells (*15–17*); transient responses occur even in response to maintained stimuli (*18*); cells have larger receptive fields (*15–17, 19*); and many cells show response attenuation (habituation) following repeated stimulus presentations at low interstimulus intervals (*15, 17*). Tactile cells were also strikingly similar to visual cells in these respects. They too represented a select population of the somatic afferent system by (i) being activated only by moving stimuli and displaying only transient responses even to maintained stimuli; (ii) possessing many large receptive fields (although there were numerous exceptions); and (iii) showing a marked tendency for habituation to a variety of tactile stimuli. These common organizational and neuronal response features are consistent with the hypothesis that the superior colliculus provides a means of utilizing information relevant to tracking behavior from at least two sensory modalities. The significant overlap of modalities (visual, somatic, and acoustic) in the intermediate layers provides a basis for modality interaction, and in a population of bimodal colliculus cells it has been shown that the area around the head in which an acoustic stimulus is effective is spatially coincident with the visual receptive field (*12*).

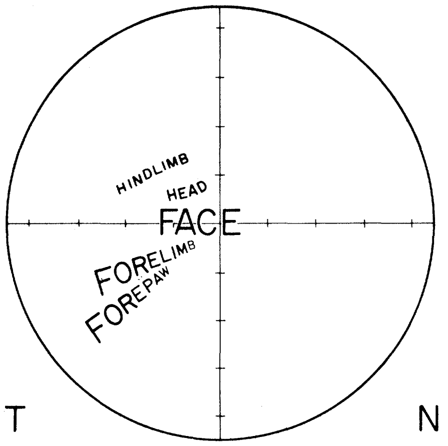

Fig. 2. Diagrammatic schema of the visuotopic-somatotopic relationship. The circular diagram represents visual space with the horizontal and vertical meridians subdivided at 20° intervals; *T*, temporal; *N*, nasal. Contralateral visual space is represented in the superior colliculus via contralateral (nasal hemiretina) and ipsilateral (temporal hemiretina) projections. This representation extends 10° or more across the vertical meridian (*12, 13*). A map of the body superimposed upon visual space was reconstructed from 85 electrode penetrations. The designation (for receptive fields) of a given contralateral body sector was placed in the appropriate position in the diagram of visual space, on the basis of the location of upper layer visual receptive fields found in the same penetrations as a given body segment. The few discrete somatic receptive fields found on the proximal body were usually in penetrations in which visual receptive fields were within 15° of, and usually inferior to, the horizontal meridian, extending from approximately 10° to 60° temporally. The representation of a portion of the face extends across the vertical meridian, as did the parafoveal visual representation to which it corresponded. The size of the lettering relates to the extent of the representation.

Since stimuli can often transmit information over different sensory channels simultaneously, the colliculus may serve as a means of extracting the most salient sensory cues that indicate stimulus location, regardless of specific modality, and of allowing the organism to make corresponding adjustments in its orientation. One of the unique features of the colliculus may be this representation of several sensory modalities, topographically coincident and all involved in a common objective. Thus, a single map of directions around the animal exists across sensory modalities, and nonvisual representations may deserve equal attention with visual for a balanced assessment of superior colliculus function.

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References and Notes

1. L. A. Palmer, A. C. Rosenquist, J. M. Sprague, in *Corticothalamic Projections and Sensorimotor Activities*, T. Frigyesi, E. Rinvik, and M. D. Yahr, Eds. (Raven, New York, 1972), p. 491.
2. S. M. Sherman, *Science* **185**, 355 (1974).

→ L. J. Poirier and C. Bertrand, *J. Comp. Neurol.* **102**, 745 (19→ F. D. Anderson and C. M. Berry, *ibid.* **111**, 195 (19→ W. R. Mehler, M. E. Feferman, W. J. H. Nauta, *Brain* **83**, 718 (19→ R. Y. Moore and J. M. Goldberg, *J. Comp. Neurol.* **121**, 109 (19→ W. E. Powell and J. B. Hatton, *ibid.* **136**, 183 (1969).

4. B. E. Stein, E. Lábos, L. Kruger, *J. Neurophysiol.* **36**, 667 (1973).
5. M. W. Fox, in *Developmental Neurobiology*, W. A. Himwich, Ed. (Thomas, Springfield, Ill., 1970), p. 553; T. T. Norton, *J. Neurophysiol.* **37**, 674 (1974).
6. B. E. Stein, B. Magalhães-Castro, L. Kruger, in *Program and Abstracts, Society for Neuroscience, 4th Annual Meeting* (1974), p. 436.

→ R. W. Rodieck, J. D. Pettigrew, P. O. Bishop, T. Nikara, *Vision Res.* **7**, 107 (1967).

8. Visual "searching" stimuli consisted of light and dark moving rectangular bars and stationary flashed lights. Visual receptive fields were mapped on the transparent hemisphere by the edge of a bar, 3° wide, moved inward from all directions in visual space until a closed area was delimited. Somatic "searching" stimuli consisted of stroking and tapping of the body. Somatic receptive fields were mapped with camel's hair brushes or calibrated von Frey hairs that vertically displaced the skin or moved across it. Acoustic stimuli consisted of clicks and handclaps, but acoustic neurons were not studied in detail.
9. Tactile stimuli were never observed to activate upper layer visual cells, and the possible influence of somatic stimuli upon responses to visual stimuli in upper layer visual cells was examined in ten examples. Simultaneous or alternating visual (moving bar or flashed light) and somatic (tapping or electrical stimulation) stimuli were delivered, but no obvious interactions were noted.
10. C. B. Bell, M. Sierra, N. Buendia, J. P. Segundo, *J. Neurophysiol.* **27**, 961 (19→ D. Jassik-Gerschenfeld, *Nature (Lond.)* **208**, 898 (19→ B. E. Stein and M. P. Arigbede, *Exp. Neurol.* **36**, 179 (1972); V. C. Abrahams and P. K. Rose, *J. Neurophysiol.* **38**, 10 (1975).

→ M. Straschill and K. P. Hoffmann, *Brain Res.* **13**, 274 (1969).

12. B. Gordon, *J. Neurophysiol.* **36**, 157 (1973).

→ S. Feldon, P. Feldon, L. Kruger, *Vision Res.* **10**, 135 (1970).

14. N. Berman and M. Cynader, *J. Physiol. (Lond.)* **224**, 363 (19→ R. H. Lane, J. H. Kaas, J. M. Allman, *Brain Res.* **70**, 413 (1974).

→ J. T. McIlwain and P. Buser, *Exp. Brain Res.* **5**, 314 (1968).

→ G. Mandl, *Brain Res.* **75**, 215 (1974).

17. P. Sterling and B. G. Wicklegren, *J. Neurophysiol.* **32**, 1 (19→ B. E. Stein and M. O. Arigbede, *Brain Res.* **45**, 437 (1972).

→ B. E. Stein, E. Lábos, L. Kruger, *Vision Res.* **13**, 2615 (1973).

19. J. T. McIlwain, *J. Neurophysiol.* **36**, 690 (1973).
20. We thank S. Sampogna and A. Golding for technical assistance. Supported by PHS grants NS-5685 and EY-571.

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Sentence Perception as an Interactive Parallel Process

Abstract. *The restoration of disrupted words to their original form in a sentence shadowing task is dependent upon semantic and syntactic context variables, thus demonstrating an on-line interaction between the structural and the lexical and phonetic levels of sentence processing.*

A normal spoken sentence can be characterized by at least four levels of description—phonetic, lexical, syntactic, and semantic. How do the listener's analyses at these different levels interact during his processing of the sentence?

This report presents evidence that sentence perception is most plausibly modeled as a fully interactive parallel process: that each word, as it is heard in the context of normal discourse, is immediately entered into the processing system at *all* levels of description, and is simultaneously analyzed at all these levels in the light of whatever information is available at each level at that point in the processing of the sentence. This is in direct contrast to the view that the direction of information flow in sentence perception is primarily serial, so that, whatever the later interactions between levels, the initial input to any higher level consists of at least a preliminary analysis conducted just at a lower level (1).

The present experiment directly tests the parallel model by combining two levels of anomaly in a sentence shadowing task. The shadowing paradigm, in which the subject repeats back speech as he hears it, provides an on-line response measure of the information available to the listener during processing. The first level of anomaly—the disruption of semantic and syntactic constraints—tests for the availability of higher-order information. The second level of anomaly, by disrupting the lexical integrity of individual words in the sentence, tests for the interaction of this higher-order information with the lower-level, lexical and phonetic analysis of the sentence.

The stimulus materials were constructed from a pool of 120 pairs of normal sentences. The second sentence in each pair contained a trisyllabic target-word. These 120 sentences were randomly assigned to three Context groups of 40 pairs each. The target-words in the Normal group were left unchanged. In the Semantic group the target-words were replaced by new words that were semantically anomalous—for example: "The new peace terms have been announced. They call for the unconditional *universe* of all the enemy forces." In the Syntactic group, the new words were syntactically anomalous as well—for example: "He thinks she won't get the letter. He's afraid he forgot to put a stamp on the *already* before he went to post it." These Context Disruptions constituted the first level of anomaly.

The 40 sentences in each Context group were then randomly assigned to four subgroups of ten sentences each. In one subgroup (labeled 0) in each Context group the target-word was left unchanged; in the other three (labeled 1, 2, and 3, respectively) the first, second, or third syllable of the target-word was changed so as to make it into a nonsense word. These Word Disruptions constituted the second level of anomaly, thus producing 12 combinations of Word and Context Disruptions, which ranged from Normal$_0$ (no contextual or lexical disruption of the target-word) to Syntactic$_3$ (the third syllable disrupted in a semantically and syntactically anomalous target-word).

The purpose of this interweaving of Word and Context disruption was to examine the effects of context on "word restoration" (that is, the restoration of disrupted words to their original form). If the interaction between higher and lower levels of analysis takes place (serially) only after the initial phonetic and lexical identification of the word, then restoration of disrupted words should be equally frequent in all Context conditions. The shadower would have no basis, in his initial repetition, for rejecting contextually anomalous restorations. However, if immediate identification does interact on-line with the semantic and syntactic context, then it becomes possible for context variables to determine word restoration frequency.

The use of the shadowing task makes possible the accurate temporal location of any interaction effects. The shadower's repetition latency, measured from the onset of a word in the input to the onset of that word in his output, specifies precisely how much of the material he could have heard before initiating his response. In this experiment 13 shadowers were used, with mean normal shadowing latencies ranging from 250 to 750 msec (2). The performance of the closer shadowers is central to the interactive parallel hypothesis. At a shadowing latency of 250 msec, their repetition of the target-words is initiated when only the first syllable could have been heard. Thus any context effects would be restricted to the initial processing of the incoming word.

The 120 stimulus sentences were recorded in random order at a rate of 160 words per minute, with a 3-second break between sentences. The subjects heard the sentences in a single session, and were instructed to shadow them as naturally as possible, while maintaining their normal shadowing distances.

Two types of restoration were distinguished in the error analysis. The critical errors are the Word Restoration (WR) errors, which are the restoration of disrupted words to their original lexical form—for