that leads to plasticity, whereas synapses from the CS "square" input may well be located close to the US "red square" synapses. It seems that not only the psychological complexity of simple models of learning has been underestimated but also the neurobiological complexity.

The argument introduced in section 5.3.1 about color opponency is also unconvincing. G&S state that neurobiology provides a description of cell populations with center/surround structure but that it cannot model the function of these cells. This seems false; the population of cells includes only red/green and blue/yellow pairings. The inference a neurobiologist draws from this is that red and green cannot be experienced in the same location at the same time because they are mutually inhibitory. The same applies to yellow and blue. Red can coexist with yellow or blue, and green also with yellow or blue. The neurobiology leads to the same conclusion about function that the psychological theory does, but by an independent route.

A restatement of the neuron doctrine that I believe more accurately reflects the views of neurobiologists might be:

> Neurobiology will come to underpin psychology. This will likely lead to substantial revolution and revision of existing psychological theories. Psychological theories not underpinned by neurobiology will be discarded in favor of those that are.

At present, neurobiology is generally reducible, through biology and biochemistry, to any desired level of explanation, although this is not possible for psychology. This version of the neuron doctrine holds that psychology will ultimately be reducible to neurobiology, and so further down to any other explanatory level, and that, because there are currently few points of contact, this is likely to entail a major revision of psychology. G&S make clear in note 30 that they are discussing reduction in principle, and that "what determines the form of the successful theory is where the best explanation is to be found" (sect. 5.3.6), although I would qualify this to include predictive power as well. Psychological concepts will be used to describe the ensemble activity of neurons but will always be directly understandable in terms of the activity of all the individual neurons in the ensemble. This version seems to give the best reading of G&S's quotes by neuroscientists such as Barlow (sect. 1.1, para. 15) and Churchland and Sejnowski (sect. 1.2, para. 6), and it is neither trivial nor unsubstantive.

Neuronal connectivity, regional differentiation, and brain damage in humans

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Abstract: When circumscribed brain regions are damaged in humans, highly specific impairments in language, memory, problem solving, and cognition are observed. Neurosurgery such as "split brain" or hemispherectomy, for example, has shown that encompassing regions, the left and right cerebral hemispheres, each control human behavior in unique ways. Observations stretching over 100 years of patients with unilateral focal brain damage have revealed, without the theoretical benefits of "cognitive neuroscience" or "cognitive psychology," that human behavior is indeed controlled by the brain and its neurons.

The arguments presented by Gold & Stoljar (G&S) have narrow definitions of the relationship between neurons and the mind, particularly when they apply to the human brain. My argument emphasizes what we know about the organization of the human mind in the brain from studying neurological and neurosurgical patients with focal brain damage (DeRenzi et al. 1968), commissurotomy (Bogen 1992; Zaidel 1990; Zaidel & Sperry 1974), and hemispherectomy, and without the benefits of what is today called *cognitive neuroscience.* The behavioral consequences of neuronal connectivity disruptions have been amply verified postmortem and with brain imaging techniques (Geschwind & Galaburda 1984).

First, not all brains are the same, even if they all have neuronal cells. *Aplysia,* rats, birds, monkeys, chimps, and humans do not have the same brains, nor do all species have the same sensory organs to process incoming stimuli. What matters is how neuronal populations have assembled into regions in each type of brain. Brain regions are defined by characteristic neuronal cell size, shape, orientation, axons, dendrites, and neurochemical and physiological processes (Zaidel et al. 1997). In humans the regions exert specialized control over behavior to an extent not seen in other animals, whether mammals or not.

Second, evolutionary adaptive changes have put constraints on the relationship between brain and mind. For example, the hallmark of human cognition is hemispheric specialization (Sperry 1974). The lateralization of speech and most components of language to the left cerebral hemisphere and of topographical knowledge and visuospatial and facial perception to the right hemisphere is unlike anything seen in animals in scope and extent. As the human brain evolved, the major interhemispheric tract of connecting fibers, the corpus callosum, grew to a size larger than in any other mammal. Similarly, as the brain evolved, the hippocampal commissure became smaller, suggesting that, rather than the abundant direct communication between the two hippocampi seen in rats, cats, or monkeys, in humans each hippocampus communicates with the ipsilateral neocortex (Amaral et al. 1984; Rosene & Van Hoesen 1987). Such an arrangement could explain why unilateral hippocampal damage in humans results in memory impairment consistent with the cognitive deficits following neocortical damage on the same side (Zaidel et al. 1994), whereas, with experimental animals, rarely if ever does memory impairment follow unilateral hippocampal damage, with bilateral damage required to produce the impairment. The encompassing region represented by each cerebral hemisphere thus controls different components of the human mind.

Third, observations on the consequences of brain damage do not require for their interpretation theories of cognitive psychology, cognitive neuroscience, or just plain psychology. When a right-handed person suffers from a stroke or a tumor affecting his left hemisphere, particularly the lower third frontal convolution (Broca's area), aphasia, a severe inability to communicate linguistically, emerges. This is simply obvious. The ancient Greeks had already observed this relationship between language and the left side of the brain.

Fourth, not all scientific pursuits of the mind have equal success in uncovering the relationship between neurons and the mind. Neuropsychology and neurology are neurodisciplines that have provided insights on mind and brain through the understanding that focal brain damage in humans fractionates the components of the mind, which, in turn, can be subjected to systematic analysis. Theories of the mind-in-the-brain gleaned by researchers in these disciplines well precede the relatively recent theories of cognitive neuroscience or cognitive science. The building blocks of the mind can be revealed by observing the alterations in neuronal connectivity.

Answers to questions such as "how does human language occur in the first place?" are elusive. The left hemisphere is critically involved; we know that much. How neurons produce language is something that we simply do not yet know (Scheibel 1984). Neuropsychologists and neurologists in collaboration with cognitive neuroscientists and scientists from neuroanatomy, immunohistochemistry, cellular biology, and experimental neuropathology will most likely discover the answer. Interdisciplinary collaborations have provided evidence for a strong relationship between neuronal density in the hippocampus, for example, and memory (Zaidel & Esiri 1996), particularly verbal memory (Rausch & Babb 1993; Sass et al. 1990), and for explicit versus implicit memory (Zaidel et al. 1998). At the same time, associations between morphological or immunohistochemical features of neurons and components of the mind are sorely missing. In any case, neuronal connectivity surely plays a critical role in producing the mind in the brain.

Amaral, D. G., Insausti, R. & Cowan, W. M. (1984) The commissural connections of the monkey hippocampal formation. *Journal of Comparative Neurology* 224:307–36. [DWZ]

Bogen, J. E. (1992) The callosal syndromes. In: *Clinical neuropsychology,* ed. K. M. Heilman & E. Valenstein. Oxford University Press. [DWZ]

DeRenzi, E., Faglioni, P. & Spinnler, H. (1968) The performance of patients with unilateral brain damage on face recognition tasks. *Cortex* 5:274–84. [DWZ]

Geschwind, N. & Galaburda, A. M. (1984) *Cerebral dominance: The biological foundations.* Harvard University Press. [DWZ]

Rausch, R. & Babb, T. L. (1993) Hippocampal neuron loss and memory scores before and after temporal lobe surgery for epilepsy. *Archives of Neurology* 50:812–17. [DWZ]

Rosene, D. L. & Van Hoesen, G. W. (1987) The hippocampal formation of the primate brain. In: *Cerebral cortex,* ed. E. G. Jones & A. Peters. Plenum Press. [DWZ]

Sass, K. J., Lenz, T., Westerveld, M., Novelly, R. A., Spencer, D. D. & Kim, J. H. (1991) The neural substrate of memory impairment demonstrated by the intracarotid amobarbital procedure. *Archives of Neurology* 48:48–52.

Sass, K. J., Spencer, D. D., Kim, J. H., Westerveld, M., Novelly, R. A. & Lenz, T. (1990) Verbal memory impairment correlates with hippocampal pyramidal cell density. *Neurology* 40:1694–97. [DWZ]

Scheibel, A. M. (1984) A dendritic correlate of human speech. In: *Cerebral dominance: The biological foundations,* ed. N. Geschwind & A. M. Galaburda. Harvard University Press. [DWZ]

Sperry, R. W. (1974) Lateral specialization in the surgically separated hemispheres. In: *The neurosciences third study program,* ed. F. O. Schmitt & F. G. Worden. MIT Press. [DWZ]

Zaidel, D. & Sperry, R. W. (1974) Memory impairment after commissurotomy in man. *Brain* 97:263–72. [DWZ]

Zaidel, D. W. (1990) Memory and spatial cognition following commissurotomy. In: *Handbook of neuropsychology,* ed. F. Boller & J. Grafman. Elsevier. [DWZ]

Zaidel, D. W. & Esiri, M. M. (1996) Hippocampal cell death. *Science* 272:1247–48. [DWZ]

Zaidel, D. W., Esiri, M. M. & Beardsworth, E. D. (1998) Observations on the relationship between verbal explicit and implicit memory and density of neurons in the hippocampus. *Neuropsychologia* 36:1049–62. [DWZ]

Zaidel, D. W., Esiri, M. M. & Harrison, P. J. (1997) Size, shape, and orientation of neurons in the left and right hippocampus: Investigation of normal asymmetries and alterations in schizophrenia. *American Journal of Psychiatry* 154:812–18. [DWZ]

Zaidel, D. W., Oxbury, S. M. & Oxbury, J. M. (1994) Effects of surgery in unilateral medial temporal lobe regions on verbal explicit and implicit memory. *Neuropsychiatry, Neurosychology, and Behavioral Neurology* 7:1–5