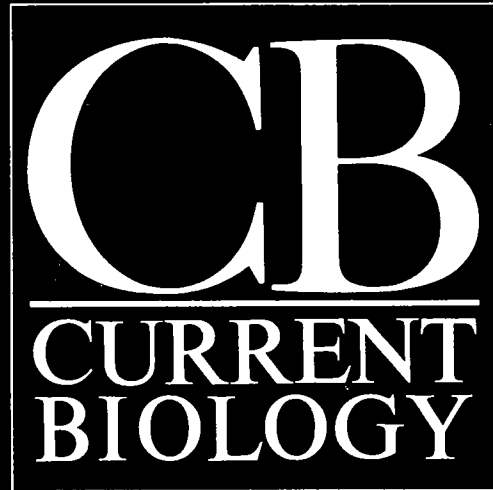


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## Motion perception and the mind–body problem

Confidence in the identity of neural and perceptual events has been increased by the use of modern experimental techniques. Now, a qualitative leap has been made in understanding the neural basis of motion perception.

One of the fundamental tenets of the mind–brain materialism subscribed to by most contemporary neurobiologists is the existence of an identity relationship between neural and perceptual events. Although the current consensus regarding such an identity can be traced to the 17th century philosophy of Spinoza, this view withered in the shadows of Cartesian dualism. Materialism flowered anew in the latter half of the 19th century with the fevered endorsement of physicist cum philosopher Gustav Fechner. His *Elemente der Psychophysik*, published in 1860 [1] and devoted to an “exact science of the functional relationship...between body and mind”, asserted that the relationship between brain and perceptual events — the ‘inner psychophysics’ — is externally manifested and thus measurable as the relationship of sensation to stimulus. These materialist sentiments echoed in the words of Ernst Mach [2] — “To every psychical there corresponds a physical, and conversely” — and were shared by many of the major figures of 19th century perceptual psychology, including Helmholtz and Hering [3]. The principles of this new view were laid out in some detail at the turn of the century by the psychologist Georg E Müller [4] who maintained that “The ground of every state of consciousness is a material process” and that “To an equality, similarity or difference in the constitution of sensations...there corresponds an equality, similarity or difference in the constitution of the psychophysical process, and conversely”. Convinced of the correctness of his beliefs and of their nearly universal acceptance, Müller presented these ideas as axiomatic, thereby transcending the burden of proof.

Proof was not readily forthcoming. Fechner recognized the technical limitations of his time and was content to measure the outer manifestations of mind–brain events. Today we see prophesy in Mach’s claim that the true mind–brain relationship will only be “ascertained by means of a physical investigation which may be extremely complicated” [2] (those who have tried such physical investigations may find some sympathy with this view). Rising to this onerous challenge, contemporary neurobiologists have brought sundry state of the art tools to the task of quantifying the inner psychophysics. Once armed with means to record the electrical activity of single neurons, physiologists set out to show that sensory stimuli known to cause specific perceptual events also cause identifiable and reproducible brain events. Implicit in this endeavor is the belief that neural activity observed in single cells or groups of cells is identical to the percept of the relevant stimulus dimension — they are merely two sides

of the same coin. Indeed, among practicing neurobiologists and students of perception, the emphasis has shifted markedly from the 19th century obsession with the existence of brain–mind identity to the more practical matter of determining which brain events are responsible for specific mind events.

To this end, the past 40 years have seen countless demonstrations of sensory receptive field properties that suggest some relevance to perception, ranging, in the case of vision, from ‘bug detectors’ in the frog retina [5] to ‘face cells’ in the primate temporal lobe [6]. Perhaps most significantly, a number of studies have paired perceptual (psychophysical) judgements with measurements of neuronal firing rate. A notable example can be found in the demonstration by Newsome and colleagues [7] that the activity of directionally selective neurons in the middle temporal visual area (MT) of monkey cortex is correlated with perceived motion. In this experiment rhesus monkeys were required to perform a direction discrimination task using moving stimuli of variable motion ‘strength’. Visual stimuli consisted of a dynamic dot display in which the strength of the motion signal was determined by the fraction of dots that moved in the same direction. The remaining dots moved in random directions. These stimuli yield a consistent psychometric relationship between motion discrimination performance and signal strength. By presenting the same set of visual stimuli while recording from single MT neurons, these investigators were also able to compute ‘neurometric’ function based on each cell’s ability to discriminate direction as a function of motion signal strength. Neurometric functions compare well to psychometric functions derived simultaneously. The essential message here is that the discriminative capacity of a single neuron covaries with that of the monkey, a result which strongly suggests that neuronal activity within MT is at least one constituent of the perceptual experience of motion. In general, it is experiments of this very sort that have provided the soundest confirmation of Müller’s dictum regarding covariance of neural and perceptual states and the substance behind Horace Barlow’s [8] ‘neuron doctrine’ for perception, in which he posited that “the activity of each single cell...is related quite simply to our subjective experience”.

“Correlations, nothing more!”, cry those dreary skeptics of psycho–neural identity. True enough, and even Newsome *et al.* [7] were careful to disenchant their readers of the notion that it is possible to assert an identity between motion perception and neural activity in area MT on the basis of their results. One may well ask whether anything

more than mere correlation lies within the grasp of empirical science. Arguably not, but philosophers of mind [9] are fond of reassuring us that criteria for 'proof' of identity claims in the physical sciences are often correlational in nature. (The relationship between temperature of a gas and energy of molecular motion is a classic example.) Given this precedent, an admirable goal may be to demonstrate that the correlation between neural and perceptual events is so close that we have no reason to expect the occurrence of one without the other. There are, in addition to direct measurements of neural activity, a number of experimental strategies that can be used to seek additional correlative evidence. If activity within a specific brain structure is believed to contribute to a specific perceptual event, one would expect to eliminate the possibility of entering that perceptual state by destroying neurons within the relevant brain structure. Conversely, it should be possible to cause the percept to occur by 'artificially' stimulating the supposed neural substrate. Both of these tactics have been applied by Newsome and colleagues in a rather forthright attempt to further define the contribution of visual area MT to perceived motion.

Brain lesion experiments have, of course, been ventured for well over 100 years and their results have been used to argue forms of mind-brain dependence, although typically these have been of an imprecise nature. Newsome and Paré [10], banking upon recent technical innovations that permit a high degree of control over the spatial extent of their lesion, have shown that motion discrimination performance (a reasonable assay of perceptual state) in rhesus monkeys depends on the integrity of area MT. Similar experiments by Siegel and Andersen [11] have yielded confirming results.

The real clincher, however, is an astonishing result reported last year by Salzman, Britten and Newsome [12]. If neural events in area MT contribute substantially to perceived motion, these investigators hypothesized, then perceived motion should hinge upon those neural events, regardless of whether there exists an appropriate stimulus in the visual field. Or, as anticipated by Barlow's Fourth Dogma bearing on the neural undercurrents of perception [8], "the full subjective experience... accompanies the neural events of sensation, *however these are caused*" (my italics). Accordingly, direct electrical microstimulation of neurons within MT, stimulation that bypasses the retina and subsequent intervening stages, should influence perceived motion. It is well known that roughly 95% of the cells in visual area MT exhibit marked directional selectivity [13] and, moreover, that these cells are clustered into cortical columns of similar direction preference [14]. By exploiting this clustering, Salzman *et al.* [12] were able to electrically stimulate small groups of cells having similar direction preferences. These investigators predicted that behavioral indices of perceived motion would be biased in favor of the preferred direction at the microstimulation site.

Rhesus monkeys were required to perform a direction discrimination task using moving stimuli of variable motion strength. These stimuli consisted of a dynamic dot display and were identical to those used for the

neurophysiological and ablation studies cited above [7,10]. Under normal conditions, these stimuli yield a consistent psychometric relationship between motion discrimination performance and signal strength [7]. Salzman *et al.* first measured the receptive field and direction preference of neurons at each microstimulation site within MT. On each trial, visual stimuli were placed within the receptive field and moved in either the preferred or opposite direction. Direction discrimination performance was assessed in trials either with or without microstimulation of MT (temporally coextensive with visual stimulus presentation).

The direction preference of a small cluster of MT neurons is first identified — rightward, for example — by recording extracellular action potentials. The same probe is then used to pass a small electrical current into the cortex, which activates the characterized neurons. The larger effect of electrical stimulation is to bias the subject's behavioral report of perceived direction of motion toward the direction represented by the stimulated neurons. Consequently, in this example, if electrical stimulation is applied while the subject views a visual stimulus having no net motion, rightward motion is reported. In other words, if neurons representing rightward motion are caused to become active, the animal will behave as though rightward motion has been perceived. For about half of the reported sites in MT, microstimulation yielded a significant behavioral response bias in favor of the direction represented among the stimulated cells. In some cases, this enforced neuronal activation produced an effect equivalent to increasing motion signal strength in the preferred direction by as much as 20%. More recently, these investigators [15] have found that microstimulation yields a response bias in favor of the direction represented by the stimulated neurons even when no stimulus is present in the visual field.

Regarded conservatively, these results show that induced activity within a small population of MT neurons provides information sufficient for the animal to make a reliable, and predictable, judgement regarding perceived motion. A headier implication is that perceptual state is clearly coupled to discrete brain events, further strengthening our belief in their identity.

Although they sharply enhance our feeling for the relationship between perceived motion and neural activity within area MT, these new results are not to be embraced without caveat. It must be recognized that electrical stimulation of MT, like movement of an image across the retina, causes a complex cascade of activity across several brain regions. It would be naive to disregard this larger pattern. Strictly speaking, stimulation of MT only shows that we can discount a contribution from the normal sequence of activation from the retina up to MT. Furthermore, Salzman *et al.* have established that activation from MT 'onward' is merely sufficient to influence behavioral indices of perceived motion. It is a far more challenging task to show that neural activity within MT is a necessary part of the perceptual experience. (MT lesions may seem to argue for the latter but, logically, no more so than the

blinding effects of a retinal lesion can be used to show that perception occurs in the retina.) Indeed, as mechanisms of sensory information processing are increasingly revealed to us, we may find that even percepts as 'simple' as a pattern of moving dots have identity in a complex network of neural events — events that are individually necessary and jointly sufficient to account for the percept.

Be that as it may, it is abundantly clear that appropriate application of this trio of experimental techniques, neurophysiological recording, discrete brain lesions and microstimulation — all paired with psychophysics — holds much promise. As exemplified by the model approach of Newsome and colleagues to motion perception, this experimental strategy will surely carry us a long way toward realizing Fechner's "relations of dependency between body and mind".

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