



A complex vector space model of single neuronal coding and experience

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ABSTRACT

A model of consciousness is proposed, in which the experience attributable to a single sensory neuron is related to its instantaneous firing rate. In that this can only be quantified within statistical limits from the incidence of spikes across multiple presentations of a stimulus, consciousness remains inaccessible to direct measurement on a single trial. In this way, the model disambiguates subjective experience from objective neural properties. The model adopts a quantum mechanical formalism, in which the state of the neuron is represented as a vector in a complex vector space.

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1. Fundamentals of experience

It is a prerequisite for any science of consciousness that the process of critical introspection can reveal common features of experience between individuals. There is broad consensus that “consciousness consists of inner, qualitative, subjective states and processes of sentience or awareness” Searle (2000).

Most individuals also report a ‘stream’ of consciousness (James, 1890): in general, sensory experience is smoothly continuous. This might be confounded by the temporal dependence that exists in the physical world. However, even when events are discontinuous, one tends to experience an illusion of continuity. One also experiences a flow of abstract ideas and associated emotions that cannot easily be attributed to the smooth dynamics of the environment.

The continuous evolution of experience sits uneasily with the discrete representation and transmission of information that characterises the neuron doctrine. Here a single spike, triggered only when membrane potential reaches threshold, depolarises the synaptic terminal to cause vesicle release (see Kandel et al., 2000). There also seems little prospect of narrowing the explanatory gap (Levine, 1983) between the objectivity of neural properties and the subjectivity of experience through incremental refinement of the neuron doctrine to incorporate experimental findings at an ever more minute subcellular scale.

2. The neuroscientific approach to consciousness

In general, neuroscientists remain untroubled by these philosophical issues (see Searle, 2000). Most are confident that subjective experience lies outside the domain of neuroscience, limiting their scope to the explanation of behaviour in terms of patterns of neural activity (see for example Hesslow, 1994). In contrast, enlightened neuroscientists prepared to acknowledge sentience as a phenomenon in need of explanation, seek the neural correlates of consciousness (NCC). An accepted definition is the “minimal set of neuronal events and mechanisms jointly sufficient for a specific conscious percept” (Koch, 2004, 1.4). The idea is to manipulate, or record spontaneous variation in, some specific aspect of experience, and attempt to identify associated changes in neural activity. The hope is that something about these objective changes is distinct and can be distinguished from the neural correlates of unconscious processing. This is an incremental approach to the problem of experience: from each experimental result, reasonable conclusions are drawn, to be confirmed in future experiment.

The approach has limitations, however. The first issue is that the quality and quantity of experience can only be transmitted imperfectly via behavioural report, limiting detailed correlation with patterns of neural activity. For example, in an authoritative review of the neural correlates of visual awareness, Rees (2007) is happy to attribute consciousness of a stimulus to an observer who is able to report its identity. In contrast “unconscious or invisible stimuli . . . are associated with responses that objectively indicate failure to discriminate the presence or identity of the stimulus (e.g. $d' \sim 0$).” This definition seems to categorise the phenomenon of ‘blindsight’ as consciousness, since a patient with a lesion in primary visual

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cortex (V1) denies visual experience, but identifies the identity of a stimulus at a rate significantly better than chance (Stoerig and Cowey, 1997). If this seems to imply that a complete reliance on report overestimates the information about which the subject is truly aware, there is also concern that there may be “phenomenal consciousness” over and above that which can be communicated to the experimenter (“access consciousness”, see Block, 2005). Most neuroscientists would argue that “there must be an explicit correspondence between any mental event and its neuronal correlates” (Koch, 2004, 1.4), even phenomenal consciousness, implying that all mind information should be in principle accessible to the neuroscientist through direct observation of brain activity. Yet one might contend that to make this assumption is to ignore, or at least trivialise the ‘hard problem’ of consciousness (Chalmers, 1996): if a model were to capture the private and subjective quality of the conscious state, then the representation of that state could not also be a directly observable neural property.

A second issue is that behavioural reports of subjective experience are themselves mediated by neural activity, confounding the interpretation of experimental results. A classic paradigm is binocular rivalry, where spontaneous transitions occur in subjective experience between incongruous images presented continuously to the two eyes. There is clearly a need for the subject to report transitions before possible neural correlates can be explored. The assumption is that those brain regions whose activity changes with varying report (e.g. areas involved in judgment of a percept against criteria for change, involved in planning and executing a motor response) are anatomically distinct from the sensory cortices themselves. The assumption may well be invalid, since even eye movements in complete darkness evoke changes in the activity of primary visual cortex (Sylvester and Rees, 2006; Sylvester et al., 2005).

A third problem with the NCC approach is in the concept of sufficiency. Most experimenters would exclude ‘enabling’ neural activity from the NCC (see Rees et al., 2002). In those sensory neurophysiologic studies in which the subject’s perceptual experience changes even as the sensory stimulus remains constant, typically the experimenter assumes that neural activity that remains unchanging is at best an unconscious representation of the stimulus. According to the definition presented above, neural activity that non-specifically enabled both percepts in a binocular rivalry paradigm could not be part of the NCC for either specific content of consciousness. As noted by Zeman (2004) this “runs the risk of missing some of the relevant action: it targets the moving tip of the iceberg of the brain activity which is required for visual experience, but it might well be that some of the unchanging background of activity is also required for visual consciousness.” Even if the validity of rejecting the unchanging background were accepted, how would the true NCC convincingly be distinguished from enabling activity that happened to correlate with specific contents of consciousness? In binocular rivalry, for example, even the activity of lateral geniculate nucleus (LGN), a thalamic relay along the visual pathway between retina and primary visual cortex (V1), changes with each subjective transition (Haynes and Rees, 2005; Wunderlich et al., 2005). Most experimenters would require a further criterion to be fulfilled before an anatomical structure could be included in the NCC, perhaps failure to elicit relevant contents of consciousness by experimental stimulation of other regions when that structure is lesioned (see Rees, 2007). By this criterion, LGN would be rejected and V1 accepted into the NCC, at least for the experience of simple phosphenes. But still many would remain unsatisfied, postulating further criteria such as ‘explicit representation’ (Koch, 2004, 2.2), which V1 seems to lack.

It seems then that deductive reasoning from experimental evidence will alone be unable to pin down any specific conscious percept to a NCC as defined. Moreover, there are qualities of con-

sciousness that are fundamental and impossible to influence by experimental manipulation (see above), qualities that would be difficult to reconcile with the neuron doctrine whatever the neural correlates of specific contents of consciousness turn out to be. More than mere correlation is needed. Rather inductive reasoning is required, based on an idea of what consciousness should be like. This is a reasonable step, since “it is not true that we can pursue science completely by using only those concepts which are directly subject to experiment” (Feynman et al., 1963, 2–6). Perhaps in any case such additional theoretical constructs will generate experimental predictions that will further clarify the NCC.

The problem confronting the science of consciousness was framed by Nagel (1993): “We lack a framework within which to interpret the information we already have, and through which to direct our search for further information that will provide fuller understanding”. In the present work, a new mathematical scheme or formalism of consciousness will be sketched that relates mind and brain, a formalism that reduces to the classical model, when scope is limited to the firing statistics of single neurons. The assumptions that will inevitably be required in developing this scheme might be considered “bridging principles . . . basic elements to our theory, not to be further explained” that “add the minimal component” to the classical description to “bring subjective experience in” (Chalmers, 1998).

3. The single neuronal code

As a starting point let us suggest, as one such bridging principle, that the contribution of a single sensory neuron to the neural code for the sensory environment parallels the relationship between a neuronal element of experience and the overall sensory percept.

Contribution to the neural code could be defined functionally as the extent to which differing behavioural responses to the sensory environment are predictable by changes in objective neuronal activity. A classic example is the experiment of Britten et al. (1992) in which recordings are made from a single neuron in macaque V5 whose responses appear selective for a particular axis of motion within a restricted region of the animal’s visual field. When there is subtle correlation of movement in either direction along the appropriate axis, within a display of otherwise random dot motion in this region, the animal’s selection of one or other alternative direction is almost entirely predictable by this single neuron’s activity. Assuming that these results apply also to the encoding of motion in humans, and adopting the bridging principle mentioned above, it would be concluded that such a V5 neuron also affords, within a limited region, a single dimension of motion experience.

In the macaque V5 example, the neuron encodes information in its firing rate, the number of spikes (depolarisation events) per unit time (see Dayan and Abbott, 2001). The simplest way to calculate a neuron’s firing rate as a function of time is to divide the trace (the record of an epoch of observation of a single neuron) into bins of fixed width, and then count the number of spikes per bin.¹ The broader the bin, the less is the firing rate contaminated by residual variation in spike timing unrelated to the information encoded. However, this method is unable to resolve true variation in firing rate that is occurring at a higher frequency (over a shorter period) than the time bin. Recording from sensory neurons it is possible to capture such variation by averaging across trials. In effect, counts are averaged from corresponding bins in traces evoked by multiple presentations of a stereotyped sensory stimulus. As the number of

¹ In a slightly more sophisticated approach, the firing rate at time t is calculated as the spike count since time $(t - w)$, where w is constant. Conceptually, a bin of width w ‘moves’ along the trace. As w increases, the calculated firing rate changes more smoothly as a function of time.

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