

# Response to Koch: Elaborations on the SCP hypothesis

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We appreciate the excellent questions raised by Koch [1] in response to our article [2] and the opportunity to elaborate on our ideas further here.

Koch asked whether we propose that it is the existence of the SCP *per se* or the activity of associated pyramidal cells that is crucial for consciousness. We noted in the legend of Fig. 3a in the original paper: ‘We propose that long-lasting synaptic activities in superficial layers, manifesting as SCPs in surface recording or low-frequency current source density (CSD) activity in superficial layers, carry large-scale information integration in the brain and contribute directly to conscious awareness.’ So the SCP is only our measurement of the responsible neuronal activities. If clever ways are found to eliminate the SCP, while leaving all responsible neuronal communications intact, or even extract the responsible information transfer and integration relationships and implement those in artificial media [3], then the quality of consciousness would remain the same in our view. However, our interest here is in the physiological underpinnings of consciousness, starting with the human brain and the brains of those species that are most similar to ours. The SCP might be a marker of such physiological activities, as we tentatively propose.

Second, Koch suggested that the information content of the SCP, and field potentials in general, is too low to support conscious experiences. ‘Think of every frame in every movie... each one corresponds to a discrete visual experience.’ We suppose that if that were true, there would never be any movies, the production of which depends precisely on the visual system’s ability to fuse adjacent stimuli into a coherent image. Existing evidence suggests that the time scale at which conscious experience seems to flow is at tens to hundreds of milliseconds [3]. Successive presentations of word stimuli get fused into a single percept if they are separated by less than 80 ms [4]. In fact, the slowness of consciousness is supported by many standard psychological paradigms, including backward masking (~100 ms), attentional blink (~500 ms), psychological refractory period (~200 ms) and postdiction (~80 ms) [5,6]. Still, the frequency range of the SCP (< 4 Hz) might seem too slow for the 80-ms-rate at which visual perception is updated. This, however, is not a problem because negative SCP shifts in different neuronal groups can be integrated into conscious experience with temporal lags much shorter than a full SCP cycle, that is, one neuronal group can become activated and contribute to conscious perception before the activity in the previous neuronal group drops and returns to baseline. Viewed in a different way, the amount of information the brain can

process at any moment is huge, but most information processing is carried out unconsciously, and the amount of information in bits per second (defined in the classical sense) accessible by consciousness is very small [7,8]. However, the information contributing to consciousness might be a privileged integrated kind that has had the chaff discarded [3,8].

Hence, the information contained in the SCP might not be less than that in the flow of consciousness. How can this view be reconciled with findings that individual neurons’ responses correlate with conscious perception? Crick wrote in 1984 [9] ‘Since a neuron can usually be made to fire by several different combinations of its inputs, the significance of its firing is necessarily ambiguous. It is thus a reasonable deduction that this ambiguity can be removed, at least in part, by the firing pattern of an assembly of cells.’ We add to this comment that concerted firing of hundreds or thousands of presynaptic neurons is the rule rather than the exception [10], which would contribute to field potentials without significant information loss, and that the real computations in a neuron are carried out at the dendrites. Therefore, field potentials might indeed be a better marker for network computations than a single neuron’s firing.

Our proposal that the information carried by specific thalamocortical feedforward pathways has to be processed by superficial-layer neurons and integrated with other activities therein to contribute to conscious awareness is not dissimilar to previous ideas that the afferent pathways, although crucial for providing a basis for the content of conscious awareness, do not contribute directly to conscious experience [3,11,12]. The same would also apply to the efferent pathways from the cerebral cortex. As for the nonspecific thalamic pathways, and the cortico-cortical feedback connections that originate from layer V and terminate in superficial layers, those were included in our model (Fig. 3a).

Our comparison with previous work was not intended to suggest that there have been no physiologically-based theories of consciousness before our proposal. In fact, Edelman, Crick and Koch were first to advocate a neurobiological approach to consciousness. A number of physiologically-based accounts have been proposed, including but not limited to reentrant [13] or recurrent [14] processing, 40-Hz synchrony [15], global neuronal workspace (which included neuronal firing, gamma-frequency activity and the P300)[12]. Further, a formal mathematical framework has been put forward that contains significant heuristic value for empirical quests on consciousness [3]. We are very fortunate indeed to follow these pioneers’ footsteps. Our idea is different from, but not mutually exclusive with previous hypotheses. For example, as discussed in our

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original paper, neuronal firing and gamma-frequency activity, as well as P300 amplitude, tend to increase during the negativity of the SCP. Moreover, the P300 might simply be a disruption of the ongoing negative SCP [16,17]. Therefore changes in these signals might accompany the change in the SCP, but we propose that it is the neuronal activities directly underlying the SCP that are most fundamental in contributing to conscious awareness. We look forward to future studies that examine this hypothesis.

Lastly, we did not claim that insects do not have consciousness, but rather suggested that it might be very different. The reasoning goes as follows: If the SCP is the substrate for consciousness in vertebrates, and it does not have a homolog in most invertebrates—to the best of our knowledge (the SCP is not a regular oscillation, though it can be entrained by oscillatory external stimuli), then a different physiological process must serve as the substrate for consciousness in invertebrates, if they are indeed conscious. If the substrates are different, then it is probable, but not necessary, that the information relationships carried by them, and therefore the quality of consciousness, would also be different. Nonetheless, as we commented previously, this is a non-testable conjecture at present.

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#### Letters

## Please don't underestimate the ventral pathway in language

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In a recent article entitled 'Pathways to language' [1], Friederici describes the dorsal pathway, along the arcuate fascicle as 'of particular importance for higher-order language processing'. She supports her notion by misquoting a recent publication of ours [2] that 'the dorsal route to be responsible for sound-to-meaning mapping', which is contrary to our findings. We found that the dorsal pathway connects regions activated during repetition of pseudo-words, that we interpreted as used for 'sensorimotor mapping of sound to articulation' [3]. By contrast, the ventral pathway along the extreme capsule connected regions active during listening to meaningful speech compared to meaningless pseudo speech, thus used for 'mapping sound to meaning'.

Friederici claims the dorsal pathway 'to be crucial for the evolution of human language, which is characterized by the ability to process syntactically complex sentences'. She

proposes a functional subdivision of the inferior frontal gyrus, 'with BA 44 supporting the processing of hierarchical structures ... and BA 45 subserving controlled semantic processes' [1]. However, BA44 might 'not be specifically related to syntactic processing' [4] and BA 45 is not only involved in semantics, but also pivotally in the acquisition of natural grammar [5] and in syntactic processing, particularly if grammar was disentangled from the semantic component [4]. Tracing studies in monkeys and tractography studies in humans [6] showed that BA 45/area 45 are connected with the temporal lobe via the ventral portion of the extreme capsule. Therefore, the ventral pathway probably plays a key role in grammar processing too.

As suggested in our paper, 'the involvement of the dorsal stream for processing of complex syntactic operations might be partially explained as a result of an increase in syntactic working memory load' [2]. Syntax and memory are hard to keep apart. The capacity to deal with hierarchically structured sequences such as AABB as in a

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