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SUBMITTED AS A LETTER TO THE EDITOR

On corticopetal-corticofugal loops of the new early filter: From cell assemblies to the rostral brainstem

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On corticopetal-corticofugal loops of the new early filter: From cell assemblies to the rostral brainstem

Selective attention affects both thalamocortically generated auditory middle-latency responses and cortically generated auditory long-latency responses, yet, up until the work of Ikeda *et al.* [1–3], no such attentional effects upon auditory brainstem responses (ABRs) had been observed [4–5]. That is, Ikeda *et al.* [1] have revealed selective attentional influences upon ABRs: In contralateral loud (100 dB SPL) noise, rare “deviant” target tone pips to the left ear exhibited a positivity in the range of waves II–VI. In addition, there were selective attentional decrements in ABRs to attended frequent “standard” non-target tone-pips relative to acoustically identical sounds that participants just ignore [1]. In quieter contralateral noise (80 dB SPL) there were no such effects [1].

Accordingly, sensory-load influences binaural mechanisms via descending corticofugal routes between subcortical processing stations. These top-down effects, in turn, affect ABR generators ipsilateral and contralateral to the attended ear via the descending auditory system [5]. Corroborative evidence of a different sort stemmed from Ikeda (2015) [2] concerning how attention affects the ABRs to binaural and monoaural stimuli. Arguably a corticofugally operated top-down early selective filtering mechanism [6], which we shall discuss, can act upon information from both ears, as becomes particularly influential under adverse conditions, e.g., loud noise.

In the studies where there is no effect of selective attention on ABRs – such as the investigation of Woldorff *et al.* [5] – what role does such a selective filtering mechanism play? This mechanism is arguably neither necessary nor apparent under the experimental conditions that Woldorff *et al.* [5] employed. In one new dichotic listening investigation with low- rather than high-level diotic noise, Ikeda [3] now better defines the stimulus conditions that permit [3] – and replicate the distinct conditions that preclude – this influence of selective attention on ABRs [3, 5]. Under conditions that preclude such an influence, Woldorff *et al.* [5], as Ikeda [3], presented higher tone-pips to the left ear and lower tone-pips to the right ear. For the first time in one experiment, Ikeda [3] reveal such stimulus conditions do not lead to an influence of selective attention on ABRs, whereas the converse stimulus conditions of lower tone-pips to the left ear and higher tone-pips to the right ear do. The point is that the attentional modulation of tone-pip ABR componentry depends upon pitch and stimulus arrangement.

We do not debate this new fact that stimulus conditions influence how selective attention affects ABRs. Instead, we rather take issue with Ikeda's (2018) Hebbian interpretation [3, 7] and elucidate how alternative models [6, 8] can explain the data of Ikeda (2018) [3].

In what ensues, there is an introduction of Hebbian theory, followed by a discussion of the two alternative models – the adaptive filtering model [8] and the new early filter model [6] – and thereafter a focus on the common assumptions of those alternative models that Ikeda challenges, addressing each challenge to each such assumption in turn There is then cautious consideration of the related view [9] that the all top-down attentional as well as experience-dependent plasticity factors are entirely cortical rather than subcortical, leading into caveats for future investigations. This discussion now embarks with Hebb.

Hebbian assumptions include that of cell assemblies [7]. Such assemblies are groups of “neurons that fire together that wire together”, due to prior Hebbian learning, in a mutually facilitatory manner persisting in a more than fleeting moment due to reverberation within that assembly. Such cell assemblies accumulate during the ascendency of information in the brain, as a counterpart to a mental representation with a persistence conducive to use in the neuronal basis of thought. In an auditory context, Ikeda (2018) [3] identifies such a cell assembly with the extant concept of an auditory object [10]. Diffuse connectivity – largely across the cortex, yet also in the diencephalon and cerebrum – Hebb proposed as necessary to cell assemblies [7:pg. xix]. Inasmuch that Hebb [7:pg. 67] notes, in the visual domain, that Area 17 of the occipital cortex lacks such necessary diffusivity by contrast with Area 18, Ikeda’s expansion [3] of Hebbian theory is that “it would be difficult to represent a perceptual object in the primary sensory cortex itself as the sensory projections up to the primary sensory cortex were not diffuse.”

Within the Hebbian notion of attention, “a hypothetical agency or process which produces selectivity, … a central facilitation of perceptual activity” [7:pg. 102], a phase-sequence, a sequence of cell assemblies, gives rise to thought. That is, a cell assembly may exist as a closed system briefly. Also, a cell assembly may facilitate the assembly of other systems, including those cell assemblies influencing motor behaviour. Selective attention is accordingly the central facilitation of cell assemblies in a phase-sequence from the attentional set of preceding assemblies. When a phase-sequence causes the central facilitation of a cell assembly before the sensory facilitation of that assembly, then an expectancy occurs [7:pg. 87] – effectively a predictive facet of selective attention. Noteworthy is that Hebb’s theory relied upon excitatory interactions eschewing not only the role of inhibition in selective attention but also inhibitory processes altogether [11]. Poignant is that, at the time when Hebb formulated his theory, neural inhibition had yet to be discovered [12]. Combining Ikeda's interpretation [3] of this Hebbian theory [7] that subcortical structures and primary auditory cortex lack the necessary diffuse connectivity with Hebb's concept of a selective attention as a phase-sequence, there is corroboration: A meta-analysis reveals the involvement of nonprimary auditory cortex as crucial to haemodynamic effects of auditory selective attention [13]. Uncontested here is such a crucial role for nonprimary auditory cortex during the effects of attention. During these effects, the rostral brainstem when implicated in attentional selectivity is arguably a subcortical servant to this and other cortical masters.

There are two distinct alternative models, the adaptive filtering model [8] and the new early filter model [6], which Ikeda's interpretation challenges: Evidence is martialled in refutation of what Ikeda [3] terms gain theory. Turning to the first alternative model, Giard *et al.* [8] defend a variant of the gain hypothesis, to which they attribute origins within the work of Hillyard and colleagues [14]. This variant is that selective attention – rather than operating by central facilitation – acts as a *gain mechanism* capable of inhibiting or gating unattended relative to attended stimulus information. This inhibition occurs at an early stage of sensory analysis kindred to the original early filter [15]. The version of the hypothesis that Giard and colleagues [8] defend assumes that, although there may be a voluntary endogenous componentry of auditory long-latency responses, there is an attentional gain applied to several distinct obligatory exogenous components. Giard and colleagues assume that this gain relies on the facilitation of to-be-attended material and the active rejection of to-be-ignored sound. This view assumes that facilitation and active rejection follow distinct time courses. Gain mechanisms can operate at several stages of sensory analysis including the cochlea and brainstem, each affecting the analysis and the representation of stimulus information. Giard and colleagues assume that there is an efferent mechanism that can modulate, under appropriate conditions, the gain at each level of processing from auditory cortices, to brainstem, to cochlea. As such, the gain in an adaptive filtering model [8] can be applied at any stage that the attentional requirements of the task determine.

Turning from Giard and colleagues' view [8], which identifies their gain mechanism with filtering, this discussion now turns to the second perspective that Ikeda [3] challenges – that is, the new early filter model [6]. By contrast to the original early filter model, which places the selective filter, albeit somewhat hesitantly, in the cochlear nuclei [15: pg.305], the new early filter model [6] assumes the top-down control of corticopetal-corticofugal loops. These loops serve as the early filter by increasing the signal-to-noise ratio at the cortex, operating early by egocentric selection [16] to which lateral inhibition is integral. This selection serves both to enhance the predicted signals and suppress unattended predicted noise. There are numerous such loops from cortex to cochlea nuclei that convey the expectancies of higher loops to lower loops. Those lower loops adjust to meet those expectancies. Although the cholinergic basal forebrain resides in a two-way feedback loop with the anterior attentional system encompassing the prefrontal cortex, projections from the cholinergic basal forebrain to the auditory and association cortices are assumed to be exclusively efferent. The cholinergic basal forebrain thus commands the auditory and association cortices. The early filter of corticofugal-corticopetal loops is, by default, wide open, such that, when stimulation is unpredictable, late selection may be more influential than early selection on cognitive performance.

It is worth considering that the top-down predictive action of corticofugal-corticopetal loops need not serve as a psychophysiological volume control leading to a gain that augments brain responses. Rather, that predictive action can lead to a neuronal phase-locking more faithful to aspects of stimulus dynamics at the level of the brainstem [17]. Such prediction leads to a more efficient neuronal coding of the stimulus during repetition suppression [18] – a sparser coding reducing the stimulus-evoked Blood-Oxygen-Level Dependent (BOLD) signal within the inferior colliculus. The new early filter model [6] assumes there are distinct forms of representation at different levels of the auditory system: for instance, the place-rate code that the inferior colliculus supports differs from that in the auditory cortex by virtue of distinct tonotopic and phase-locking characteristics as a function of centre frequency at those levels.

Although Ikeda [3] again establishes an early effect of selective attention on the ABR, thus supporting the alternative models [6, 8], Ikeda [3] challenges several assumptions made by both those models, i.e.: Selective attention can affect both the brainstem and primary auditory cortex. There are different forms of representations during processing at distinct levels of the auditory system. Selective auditory attention relies mostly on efferent pathways. This selective attention can involve not just inhibitory but also excitatory processes (cf., [7]). The following addresses challenges to each of these assumptions in turn.

Striking accord somewhat with Ikeda's challenge [Ike18] that an involvement of nonprimary auditory cortex is crucial to auditory selective attention [13], the new early filter model [6] does assume that primary auditory cortex can be subject to top-down control during selective attention. Such an assumption of exclusive top-down control of primary auditory cortex would have been untenable for the new early filter model. Germane are the differences in top-down cholinergic projections from the basal forebrain to the primary and nonprimary auditory cortex, which may have functional consequences [19]. However, in countenance to the supposed emphasis on the primary auditory cortex of the new early filter [6, 20], the model also allows for top-down cholinergic influences upon both primary and nonprimary auditory cortex during selective attention, as well as upon association areas.

In Ikeda's further challenge [3] about which structures are affected by attention supporting what forms of representation, with respect to the adaptive filtering model [8] and the new early filter model [6], Ikeda [3:pg. 497] conjectures the hypothesis that "According to the gain theory of selective attention […] the attention effect on neuronal processing (i.e., facilitation or inhibition) would be *consistent* between the auditory cortical and subcortical neurons." In test of this hypothesis, Ikeda [3:pg. 501] asserts that the distinct pattern of attentional modulation of the componentry of the auditory brainstem responses – and arguably cortically generated long-latency responses – "conflicts with the *coherent* modulation of both cortical and subcortical neurons by auditory efferent pathways." Pivotal is what "consistent" or "coherent" means, as hinges the relation of the hypothesis to the adaptive filtering model [8] (M-. H. Giard, Personal communication, April 10th, 2018) and the new early filter model [6].

Mapping the hypothesis onto a well-designed experiment, Ikeda [3] derives and tests a hypothesis: If “consistent” and “coherent” mean identical in that hypothesis then an attentional modulation of componentry, regardless of tonal pitch or stimulus arrangement, will be qualitatively similar whether the componentry is of the auditory brainstem or the arguably cortically generated long-latency response. This, the ABR data do not show [3], as is Ikeda’s challenge.

However, neither in the new early filter model nor in the adaptive filtering model (M-. H. Giard, Personal communication, April 10th, 2018) is there the assumption that the object receives full representation at each level of processing. Consider if, rather, as both the adaptive filtering model [8] and the new early filter model [6] assume, there are different neuronal representations of the auditory stimulus, which are subject to distinct forms of processing at different levels in the auditory system. If so, then consistency and coherence take on different meanings: The extent of the modulation at different levels could depend not just on the configuration and content of the stimuli but also upon task requirements (e.g., attending to pitch), such that there can be conditions for an efferent mechanism to modulate processing at the level of the brainstem.

Ikeda’s challenge to the role of efferent pathways in selective attention has the questionable underpinnings of a non-identical pattern of effects of selective attention upon cortically generated long-latency responses and ABRs. Rather, an influence of auditory efferent pathways on cortical and subcortical pathways still seems feasible. Such an influence is perhaps constrained to a route (secondarily) modulating the (ascending lemniscal input to the) left inferior colliculus subcortically, at least for pitch. Some views schematise these left and right pathways separately in presentation of corticopetal-corticofugal loops within the human ascending and descending auditory system (e.g., [6, 17]). As such, qualifications to the views under challenge [6, 8] could account for the pattern of ABR attentional modulations without recourse to the Hebbian perspective [3, 7].

For instance, processing of different stimulus attributes may exhibit a distinct lateralization of processing in the rostral brainstem from that shown in the cortex. Germane to this discussion is localizer task data [18] during a pitch contour direction detection task in which binaural speech stimuli significantly activate the left not the right Inferior Colliculus (IC) of the auditory brainstem. Is there a specialisation of the sound-contralateral left IC for pitch processing? Is it that attention to pitch influences left IC only? The EEG Frequency Following Response (FFR) phase-locks to the ascending frequency of the second harmonic of a chirp up until an individually variable limit, which ranges from 881 to 1348 Hz in young adults [21]. Noting phase-locking in the IC breaks-down around such a limit [21], is this left more than the right IC particularly sensitive to attention to frequency up until this limit? Up until this frequency, presenting sounds to the right ear rather than the left ear would thus produce stronger attentional effects. Those effects would modulate phase-locking in the left IC. The tones in a previous investigation [5] would affect place-coding rather than phase-locking in the IC. As such, tones in this previous investigation [5], if receiving a differential attentional processing within the IC, would involve small rather than broad neuronal populations in the IC, thus not affecting scalp EEG as substantially. Ikeda [3] reveals unconducive to attentional effects in the brainstem is a stimulus arrangement with higher frequency tones to the left ear and lower frequency tones to the right ear, kindred to this absence of attentional ABR findings in some prior work [5]. However, the absolute rather than the interaural relative pitches of that prior investigation [5] may account for the absence of attentional ABR effects. Arguably stimulation of the left IC by higher frequency tones in the right ear by contrast thus produces phase-locking of broad neuronal populations that are subject to efferent attentional modulations. Intriguingly, Ikeda [3] indicates that the relative interaural pitch, rather than absolute pitch, is crucial to attentional modulation.

A key shortcoming of Ikeda's Hebbian interpretation [3] remains the absence of the theoretical possibility of (selective attentional influences on) neuronal inhibition. Inhibitory processes are ubiquitous in the cortex [22] and a facet of binaural interactions at the level of the auditory brainstem [23]. The Hebbian concept of a brain without inhibition rather better describes a brain that exhibits epileptiform activity [22]. If such neural inhibition plays a role in attentional modulations of ABRs [1–3], such data are more reconcilable with the alternative models [6, 8] than with Hebbian theory [7].

The deepest challenge of these alternative models is the replication of the conditions for the elusive effects of attention on ABRs. Such replication should motivate new explanatory assumptions such as a crucial role of the left IC in the functional connectivity for attention to pitch.

From addressing Ikeda's challenges, the discussion now shifts to a related perspective. Upon a recent tide of scepticism concerning the influence of selective attention on subcortical processing, waiting in the wings is a different perspective that the apparent top-down attentional as well as experience-dependent plasticity factors that seem to affect the brainstem are entirely cortical [9]. Accordingly, the influence of these factors on the rostral brainstem seem miscast: Considering the structure of a person’s magnetoencephalogram during the presentation of a sustained vowel sound of a reveals frequency following response (FFR) generators that phase-lock to the acoustical stimulus content not only in the subcortical structures of the medial geniculate, inferior colliculus, and cochlear nucleus, but also in the auditory cortices bilaterally [24]. Noteworthy is that a right cortical FFR source rather than left cortical or subcortical FFR sources index musicianship and performance on a pitch discrimination task [24]. As such, a possible inference is that experience-dependent plasticity affects this FFR. An even bolder inference would be that the attentional influences on FFR called into question [9], if genuine, could be cortically rather than subcortically mediated. Further, phase-locking in the inferior colliculus, without cortical involvement can be obtained from EEG measurements with higher harmonics at frequencies over 150 Hz [25]. To be determined is whether the presence of cortical FFR generation for the ca.100 Hz fundamental [25] in the absence of FFR for higher harmonics is due to modes of the fundamental receiving less cortical processing rather than the frequency of those partials *per se*.

Caveats thus include that higher harmonic stimulus content is ideal for investigations of top-down attentional influences on phase-locked responses in the rostral brainstem. Another caveat to bear in mind is that the stimuli content should be less than 881 Hz to activate broad neuronal populations in both inferior colliculi thus strongly affecting responses measurable at the scalp [6, 21].

To sum-up, a re-evaluation of Ikeda’s hypothesis that attention’s effect on neuronal processing (i.e., facilitation or inhibition) would be *consistent* between the auditory cortical and subcortical neurons accords with, rather than militates against as

Ikeda [3] asserts, both the adaptive filtering model [8] and the new early filter model [6]. However, the definition of consistent must permit that there are different neuronal representations of the auditory stimulus, which are subject to distinct forms of processing at different levels in the auditory system. Ikeda's data support such a form of consistency within his hypothesis. Accordingly, some forms of processing can be subject to top-down attentional influences – not only from facilitatory but also from inhibitory processes – mostly via the descending auditory system

In assessment, the adaptive filtering model [8] and the new early filter model [6] offer a more plausible explanation of Ikeda's influence of stimulus conditions on the attentional influence upon ABRs than Ikeda's Hebbian interpretation [3]. Ikeda has improved the definition of the stimulus conditions that permit [3], and the different conditions that preclude, an influence of selective attention on ABRs [3, 5]. The adaptive filtering model [8] and the new early filter model [6] – by contrast to a Hebbian interpretation [3, 7] – may well accommodate a tenable explanation of this improved definition.

As to where the state-of-the-art is going, replication of the elusive effects of attention on ABRs may well employ the caveats for the choice of stimuli reviewed in the foregoing to motivate new explanatory assumptions for the new early filter model [6]. Such assumptions could include a crucial role of the left IC in the functional connectivity for attention to pitch.

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AUTHOR CONTRIBUTIONS

Both JM and TC made substantial contributions to the concept and interpretation in drafting the manuscript, approved the submitted materials, and have agreed to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

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Covering Letter

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August 10th, 2018

Dear Prof. Jakowec,

RE: **Discontinuity of early and late event-related brain potentials for selective attention in dichotic listening**

Please find within the enclosure a manuscript NR-S-18-00384, "On corticopetal-corticofugal loops of the new early filter: From cell assemblies to the rostral brainstem", which I have co-authored with my collaborator John Marsh. We would wish to submit this manuscript as a Letter to the Editor of *NeuroReport*. We would be honoured should you oversee a peer-review process regarding this manuscript. The manuscript concerns a recent article by Dr Ikeda that appeared under Integrative Systems:

> Ikeda K. Discontinuity of early and late event-related brain potentials for selective attention in dichotic listening. *NeuroReport* 2018; **29**:495–503. doi:10.1097/wnr.0000000000001004

We do not debate the new fact that stimulus conditions influence how selective attention affects Auditory Brainstem Responses. Instead, we rather take issue with Ikeda's (2018) Hebbian interpretation and elucidate how alternative models, including our own, can explain the data of Ikeda (2018). In respect to these extant models of auditory neurocognition, this Letter manuscript would unite the interests of your Integrative Systems readership to the interests of those researching Cognitive Neuroscience and Neuropsychology.

We would hope that Dr Ikeda offers your readership a reply enlivening the scientific debate, in which our scholarly interaction has already proved productive. Should such a reply be forthcoming, we would also be pleased to address such a rejoinder.

Dr Ikeda's article states that all participants provided their informed consent before the experiment, and this study was in accordance with the Declaration of Helsinki as approved by the ethics committee in Tokyo Gakugei University. The Letter manuscript is 19 pages long. This manuscript is not under consideration for publication elsewhere. I very much hope that this Letter manuscript is to your interest and I do look forward to hearing from you.

Yours sincerely,

Thomas Campbell

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