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# NeuroReport

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

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1 SUBMITTED AS A LETTER TO THE EDITOR

2 Running head: ATTENTION AND ABRS

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

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

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

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

43 In the studies where there is no effect of selective attention on ABRs – such as  
44 the investigation of Woldorff *et al.* [5] – what role does such a selective filtering  
45 mechanism play? This mechanism is arguably neither necessary nor apparent under

46 the experimental conditions that Woldorff *et al.* [5] employed. In one new dichotic  
47 listening investigation with low- rather than high-level diotic noise, Ikeda [3] now  
48 better defines the stimulus conditions that permit [3] – and replicate the distinct  
49 conditions that preclude – this influence of selective attention on ABRs [3, 5]. Under  
50 conditions that preclude such an influence, Woldorff *et al.* [5], as Ikeda [3], presented  
51 higher tone-pips to the left ear and lower tone-pips to the right ear. For the first time in  
52 one experiment, Ikeda [3] reveal such stimulus conditions do not lead to an influence  
53 of selective attention on ABRs, whereas the converse stimulus conditions of lower  
54 tone-pips to the left ear and higher tone-pips to the right ear do. The point is that the  
55 attentional modulation of tone-pip ABR componentry depends upon pitch and  
56 stimulus arrangement.

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

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

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

83           Within the Hebbian notion of attention, “a hypothetical agency or process  
84 which produces selectivity, ... a central facilitation of perceptual activity” [7:pg. 102],  
85 a phase-sequence, a sequence of cell assemblies, gives rise to thought. That is, a cell  
86 assembly may exist as a closed system briefly. Also, a cell assembly may facilitate the  
87 assembly of other systems, including those cell assemblies influencing motor  
88 behaviour. Selective attention is accordingly the central facilitation of cell assemblies  
89 in a phase-sequence from the attentional set of preceding assemblies. When a phase-  
90 sequence causes the central facilitation of a cell assembly before the sensory  
91 facilitation of that assembly, then an expectancy occurs [7:pg. 87] – effectively a  
92 predictive facet of selective attention. Noteworthy is that Hebb’s theory relied upon

93 excitatory interactions eschewing not only the role of inhibition in selective attention  
94 but also inhibitory processes altogether [11]. Poignant is that, at the time when Hebb  
95 formulated his theory, neural inhibition had yet to be discovered [12]. Combining  
96 Ikeda's interpretation [3] of this Hebbian theory [7] that subcortical structures and  
97 primary auditory cortex lack the necessary diffuse connectivity with Hebb's concept  
98 of a selective attention as a phase-sequence, there is corroboration: A meta-analysis  
99 reveals the involvement of nonprimary auditory cortex as crucial to haemodynamic  
100 effects of auditory selective attention [13]. Uncontested here is such a crucial role for  
101 nonprimary auditory cortex during the effects of attention. During these effects, the  
102 rostral brainstem when implicated in attentional selectivity is arguably a subcortical  
103 servant to this and other cortical masters.

104           There are two distinct alternative models, the adaptive filtering model [8] and  
105 the new early filter model [6], which Ikeda's interpretation challenges: Evidence is  
106 martialled in refutation of what Ikeda [3] terms gain theory. Turning to the first  
107 alternative model, Giard *et al.* [8] defend a variant of the gain hypothesis, to which  
108 they attribute origins within the work of Hillyard and colleagues [14]. This variant is  
109 that selective attention – rather than operating by central facilitation – acts as a *gain*  
110 *mechanism* capable of inhibiting or gating unattended relative to attended stimulus  
111 information. This inhibition occurs at an early stage of sensory analysis kindred to the  
112 original early filter [15]. The version of the hypothesis that Giard and colleagues [8]  
113 defend assumes that, although there may be a voluntary endogenous componentry of  
114 auditory long-latency responses, there is an attentional gain applied to several distinct  
115 obligatory exogenous components. Giard and colleagues assume that this gain relies  
116 on the facilitation of to-be-attended material and the active rejection of to-be-ignored

117 sound. This view assumes that facilitation and active rejection follow distinct time  
118 courses. Gain mechanisms can operate at several stages of sensory analysis including  
119 the cochlea and brainstem, each affecting the analysis and the representation of  
120 stimulus information. Giard and colleagues assume that there is an efferent mechanism  
121 that can modulate, under appropriate conditions, the gain at each level of processing  
122 from auditory cortices, to brainstem, to cochlea. As such, the gain in an adaptive  
123 filtering model [8] can be applied at any stage that the attentional requirements of the  
124 task determine.

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



141 wide open, such that, when stimulation is unpredictable, late selection may be more  
142 influential than early selection on cognitive performance.

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

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

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

174 In Ikeda’s further challenge [3] about which structures are affected by attention  
175 supporting what forms of representation, with respect to the adaptive filtering model  
176 [8] and the new early filter model [6], Ikeda [3:pg. 497] conjectures the hypothesis that  
177 “According to the gain theory of selective attention [...] the attention effect on  
178 neuronal processing (i.e., facilitation or inhibition) would be *consistent* between the  
179 auditory cortical and subcortical neurons.” In test of this hypothesis, Ikeda [3:pg. 501]  
180 asserts that the distinct pattern of attentional modulation of the componentry of the  
181 auditory brainstem responses – and arguably cortically generated long-latency  
182 responses – “conflicts with the *coherent* modulation of both cortical and subcortical  
183 neurons by auditory efferent pathways.” Pivotal is what “consistent” or “coherent”  
184 means, as hinges the relation of the hypothesis to the adaptive filtering model [8] (M-  
185 H. Giard, Personal communication, April 10th, 2018) and the new early filter model  
186 [6].

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

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

204 Ikeda’s challenge to the role of efferent pathways in selective attention has the  
205 questionable underpinnings of a non-identical pattern of effects of selective attention  
206 upon cortically generated long-latency responses and ABRs. Rather, an influence of  
207 auditory efferent pathways on cortical and subcortical pathways still seems feasible.  
208 Such an influence is perhaps constrained to a route (secondarily) modulating the  
209 (ascending lemniscal input to the) left inferior colliculus subcortically, at least for  
210 pitch. Some views schematise these left and right pathways separately in presentation

211 of corticopetal-corticofugal loops within the human ascending and descending  
212 auditory system (e.g., [6, 17]). As such, qualifications to the views under challenge [6,  
213 8] could account for the pattern of ABR attentional modulations without recourse to  
214 the Hebbian perspective [3, 7].

215           For instance, processing of different stimulus attributes may exhibit a distinct  
216 lateralization of processing in the rostral brainstem from that shown in the cortex.  
217 Germane to this discussion is localizer task data [18] during a pitch contour direction  
218 detection task in which binaural speech stimuli significantly activate the left not the  
219 right Inferior Colliculus (IC) of the auditory brainstem. Is there a specialisation of the  
220 sound-contralateral left IC for pitch processing? Is it that attention to pitch influences  
221 left IC only? The EEG Frequency Following Response (FFR) phase-locks to the  
222 ascending frequency of the second harmonic of a chirp up until an individually  
223 variable limit, which ranges from 881 to 1348 Hz in young adults [21]. Noting phase-  
224 locking in the IC breaks-down around such a limit [21], is this left more than the right  
225 IC particularly sensitive to attention to frequency up until this limit? Up until this  
226 frequency, presenting sounds to the right ear rather than the left ear would thus  
227 produce stronger attentional effects. Those effects would modulate phase-locking in  
228 the left IC. The tones in a previous investigation [5] would affect place-coding rather  
229 than phase-locking in the IC. As such, tones in this previous investigation [5], if  
230 receiving a differential attentional processing within the IC, would involve small  
231 rather than broad neuronal populations in the IC, thus not affecting scalp EEG as  
232 substantially. Ikeda [3] reveals unconvincing to attentional effects in the brainstem is a  
233 stimulus arrangement with higher frequency tones to the left ear and lower frequency  
234 tones to the right ear, kindred to this absence of attentional ABR findings in some

235 prior work [5]. However, the absolute rather than the interaural relative pitches of that  
236 prior investigation [5] may account for the absence of attentional ABR effects.  
237 Arguably stimulation of the left IC by higher frequency tones in the right ear by  
238 contrast thus produces phase-locking of broad neuronal populations that are subject to  
239 efferent attentional modulations. Intriguingly, Ikeda [3] indicates that the relative  
240 interaural pitch, rather than absolute pitch, is crucial to attentional modulation.

241 A key shortcoming of Ikeda's Hebbian interpretation [3] remains the absence  
242 of the theoretical possibility of (selective attentional influences on) neuronal  
243 inhibition. Inhibitory processes are ubiquitous in the cortex [22] and a facet of binaural  
244 interactions at the level of the auditory brainstem [23]. The Hebbian concept of a brain  
245 without inhibition rather better describes a brain that exhibits epileptiform activity  
246 [22]. If such neural inhibition plays a role in attentional modulations of ABRs [1–3],  
247 such data are more reconcilable with the alternative models [6, 8] than with Hebbian  
248 theory [7].

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

253 From addressing Ikeda's challenges, the discussion now shifts to a related  
254 perspective. Upon a recent tide of scepticism concerning the influence of selective  
255 attention on subcortical processing, waiting in the wings is a different perspective that  
256 the apparent top-down attentional as well as experience-dependent plasticity factors  
257 that seem to affect the brainstem are entirely cortical [9]. Accordingly, the influence of

258 these factors on the rostral brainstem seem miscast: Considering the structure of a  
259 person's magnetoencephalogram during the presentation of a sustained vowel sound of  
260 a reveals frequency following response (FFR) generators that phase-lock to the  
261 acoustical stimulus content not only in the subcortical structures of the medial  
262 geniculate, inferior colliculus, and cochlear nucleus, but also in the auditory cortices  
263 bilaterally [24]. Noteworthy is that a right cortical FFR source rather than left cortical  
264 or subcortical FFR sources index musicianship and performance on a pitch  
265 discrimination task [24]. As such, a possible inference is that experience-dependent  
266 plasticity affects this FFR. An even bolder inference would be that the attentional  
267 influences on FFR called into question [9], if genuine, could be cortically rather than  
268 subcortically mediated. Further, phase-locking in the inferior colliculus, without  
269 cortical involvement can be obtained from EEG measurements with higher harmonics  
270 at frequencies over 150 Hz [25]. To be determined is whether the presence of cortical  
271 FFR generation for the ca.100 Hz fundamental [25] in the absence of FFR for higher  
272 harmonics is due to modes of the fundamental receiving less cortical processing rather  
273 than the frequency of those partials *per se*.

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

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

282 Ikeda [3] asserts, both the adaptive filtering model [8] and the new early filter model  
283 [6]. However, the definition of consistent must permit that there are different neuronal  
284 representations of the auditory stimulus, which are subject to distinct forms of  
285 processing at different levels in the auditory system. Ikeda's data support such a form  
286 of consistency within his hypothesis. Accordingly, some forms of processing can be  
287 subject to top-down attentional influences – not only from facilitatory but also from  
288 inhibitory processes – mostly via the descending auditory system

289           In assessment, the adaptive filtering model [8] and the new early filter model  
290 [6] offer a more plausible explanation of Ikeda's influence of stimulus conditions on  
291 the attentional influence upon ABRs than Ikeda's Hebbian interpretation [3]. Ikeda has  
292 improved the definition of the stimulus conditions that permit [3], and the different  
293 conditions that preclude, an influence of selective attention on ABRs [3, 5]. The  
294 adaptive filtering model [8] and the new early filter model [6] – by contrast to a  
295 Hebbian interpretation [3, 7] – may well accommodate a tenable explanation of this  
296 improved definition.

297           As to where the state-of-the-art is going, replication of the elusive effects of  
298 attention on ABRs may well employ the caveats for the choice of stimuli reviewed in  
299 the foregoing to motivate new explanatory assumptions for the new early filter model  
300 [6]. Such assumptions could include a crucial role of the left IC in the functional  
301 connectivity for attention to pitch.

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307

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308

Both JM and TC made substantial contributions to the concept and interpretation in

309

drafting the manuscript, approved the submitted materials, and have agreed to be accountable

310

for all aspects of the work in ensuring that questions related to the accuracy or integrity of any

311

part of the work are appropriately investigated and resolved.

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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](https://doi.org/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,

Tom Campbell.

**Dos. Ph.D. Tom Campbell**

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