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

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Running head: ATTENTION AND ABRs

On corticopetal-corticofugal loops of the new early filter: From cell assemblies to the
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 10th, 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

AUTHOR CONTRIBUTIONS

308

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309

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

310

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311

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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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