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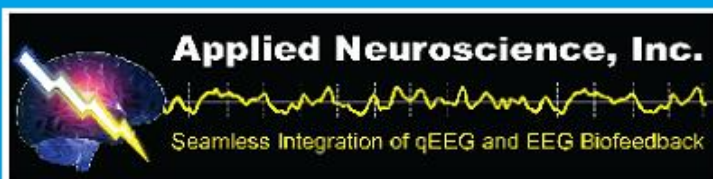
Synchrony Measures and Non-Homotopic: Do Synchrony Measures Between Non-Homotopic Areas Make Sense?

David A. Kaiser, PhD

Coactivation and synchronization of disparate brain areas underlies much of cognition, normal as well as pathological, making measures of synchronization between cortical sites of obvious interest to clinicians and neuroscientists alike. Coherence, an electroencephalic measure of synchrony, has been around for decades (Walter, 1968). Comodulation, an amplitude-based measure of cortical synchrony, is a recent addition to this field of study (Kaiser, 1994; Sterman & Kaiser, 1999). Coherence measures stationarity of the *phase* difference between two signals at each frequency whereas comodulation measures stationarity of the *magnitude* difference between two signals at each frequency. Activity in common between two electrode sites can be characterized in complementary fashion, in terms of either shared frequencies or shared timing, respectively, or both. Electrode pairings can be one of four types: strictly ipsilateral (intrahemispheric; e.g., F7-F3), midline-ipsilateral (e.g., F7-Fz), homotopic (interhemispheric at homologous sites; e.g., F7-F8), and heterotopic (interhemispheric at non-homologous sites; e.g., F7-F4). Using the 10-20 electrode placement system, a total of 171 pairings are possible, out of which 64 are contralateral (i.e., between a left hemisphere site and right hemisphere site). Of these 64, 8 are homotopic (Fp1-Fp2, F7-F8, F3-F4, T3-T4, C3-C4, T5-T6, P3-P4, O1-O2) and 56 are heterotopic (see Figure 1). Given the organization of the cortex, however, it may not make

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FIGURE 1. Example of homotopic (F3-F4) and heterotopic (F3-P4) EEG site-pairs.
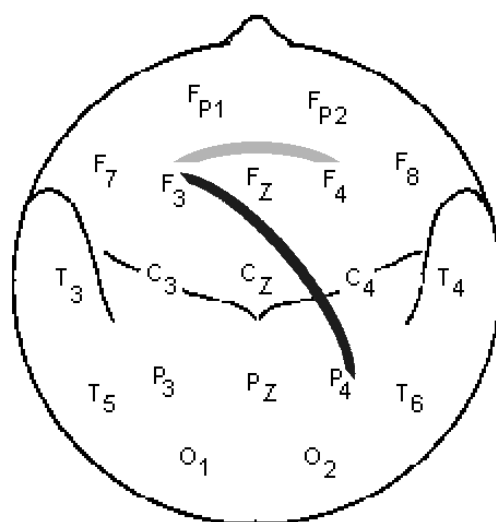
much sense to examine activity between heterotopic pairs unless a direct (monosynaptic) connection between the brain areas can be established. Without a direct pathway, coactivation or synchronization must reflect the summation or conjunction of multiple connections (i.e., homotopic and ipsilateral), and therapeutic interventions and interpretations would need to be adjusted accordingly.

Establishing direct connections for each of the 56 heterotopic sites will not be easy. The brain is divided into two cerebral hemispheres connected by a series of commissures, or axon bundles, the most conspicuous being the corpus callosum (in placental mammals; the corpus callosum is absent in marsupials and monotremes). The corpus callosum is a very large collection of nerve fibers, larger than all descending and ascending tracts combined. Its central role in psychological unity was recognized early by Willis (1664) and Lancisi (1713) and others, based on neuroanatomical considerations alone–its large size, central location, and widespread connections (cited in Harris, 1995; Tomasch, 1954; Bogen, 1985). These insights were dismissed or ignored in the 19th and early 20th centuries as an accumulation of negative findings and ambiguous results in animal research piled up (e.g., Akelaitis, 1949).

Roughly 70 to 80% of the cortex is callosally connected (Kaas, 1995), although the number of callosal neurons is no more than 1 to 2% of the to-

tal. Callosal neurons are thought to make "minimal direct contribution to the cortical EEG" due to their scarcity (Matsuo, Ono, Baba, & Ono, 2002), but their impact in neurocognitive function should not be underestimated. Callosal neurons are unique and consequential, exhibiting greater spine density and much longer apical and basal dendritic arbors than ipsilateral neurons (Soloway, Pucak, Melchitzky, & Lewis, 2002) with an ultrastructure and synaptology unlike other neurons. For instance, they exhibit more inhibitory axosomatic synapses than thalamacortical and corticocortical neurons among other features (Farinas & DeFelipe, 1991). Evidence of their significant role in cognition is perhaps best demonstrated by its arrest: the corpus callosum is greatly responsible for the spread of generalized seizures (Erickson, 1940; Lewandowsky, 1907). In 1949, McCulloch quipped that seizure propagation from one hemisphere to the other "was the only demonstrable function of the corpus callosum." (Generalized seizures can also spread through the smaller anterior commissure, as well as through brainstem or spinal commissures [Frost, Baldwin, & Wood, 1958].)

The vast majority of the interhemispheric connections in the adult human forebrain (around 94%) pass through the corpus callosum. The anterior commissure provides about 5% and the remaining forebrain commissures hippocampal, posterior and the habenular, combined for less than 1% (Lamantia & Rakic, 1990). (The central nervous system outside of the forebrain is also connected by spinal and brainstem commissures.) The corpus callosum consists of an estimated 200 million axons (Tomasch, 1954; Aboitiz, Scheibel, Fisher, & Zaidel, 1992). Compare 200 million to 20 billion, the average number of neocortical neurons in the adult human (Pakkenberg & Gundersen, 1995, 1997; Braendgaard, Evans, Howard, & Gundersen, 1990). Most of the 160 trillion synapses in the adult brain (Tang, Nyengaard, De Groot, & Gundersen, 2001) are ipsilateral connections, serving intrahemispheric functions. This fact alone, the hundred-fold difference between intrahemispheric and interhemispheric connections, is relevant to EEG analysis in that midline-ipsilateral synchrony is likely the product of ipsilateral connectivity alone, and should be considered as such. Notwithstanding, 200 million interhemispheric fibers can produce incredible complexity. The richness of the visual world is communicated to the human brain via a mere million optic fibers, for comparison.

Both Tomasch and Aboitiz relied on light microscopy for their surveys, except for a single case in Aboitiz et al. (1992) where an electron microscope was used. Innocenti (1986) speculated that cell counts will triple as optics advance. Although callosal fibers can be as narrow as 0.1

microns in diameter in humans, below the resolution of a light micro-scope, myelinated fibers (0.6 microns and larger) are readily light-resolv-able and at least 95% of callosal fibers are myelinated (except in the genu, the anterior section of the corpus callosum that connects prefrontal cor-tex; where 84% of the fibers are myelinated; Aboitiz et al., 1992). Aboitiz' single examination using an electron microscope found very few axon diameters (perhaps 20%) that would not register with the cen-tury-old technology light microscope. Accordingly, the primary source of error with neuronal counts is not with the optics but in the sampling and statistical techniques (Pakkenberg & Gundersen, 1995). All things considered, the 200 million estimate is likely to stand indefinitely.

Cortico-cortical connections are either homotopic, heterotopic, or ipsilateral. The term "homotopic" is derived from the Greek: "homo" means same, "topos" means place. Homotopy may be considered in terms of anatomical location (e.g., same lobe or Brodmann area) or sen-sory representation (e.g., same area of a visual field). Kaas (1995) refers to heterotopic connections as those between mismatched locations in sensory representation, regardless of whether they link same or different brain regions. For instance, connections between the left occipital lobe (corresponding to electrode site O1) and a visual area in the right parietal lobe (e.g., site P4) where the same part of the visual field was represented would be called homotopic. Innocenti (cf. review, 1986) and most other investigators base the terminology on neuroanatomical distinctions, not representational ones. For the purposes of EEG analysis, the latter terminology will be used.

Homotopic connections link one area in a hemisphere to the similarly located area in the other hemisphere. The homotopic area is called its homologue and lateralized brain regions such as Broca's area have homologues in the other (here, right) hemisphere based on spatial coordinates and not on functional parallels. Homotopic connections are thought, among other functions, to provide midline fusion in secondary sensory cortices, ensuring unitary perception of sensory space (e.g., Aboitiz et al., 1992). Heterotopic connections link one area in a hemi-sphere to a different region in the other hemisphere. Homotopic connec-tions link homologues (e.g., left and right posterior temporal lobe, T5 and T6), heterotopic connections link heterologues (e.g., left temporal and, say, right frontal lobes; e.g., T3 and F4). Finally, because scalp electrodes are limited in their spatial resolution, a fourth term for callosal connection is needed in our level of analysis. "Homoareal" connections are defined as callosal connections between non-homotopic contralateral sites, which are proximal to each homologue and thus not truly heterotopic (see Fig-

ure 2). For instance, a fiber projecting from area 18 (e.g., O1) in the left hemisphere to the adjacent region in area 19 (e.g., P6) in the right hemisphere, while not strictly homotopic, should not be considered heterotopic, especially from the perspective of scalp recordings. It is homoareal, detectable by the electrode above the homotopic site.

The general principle of callosal homotopy–that the corpus callosum unites "corresponding and identical regions" (Meynert, 1872; p. 405)– was initially proposed by Arnold (1838-1840) in his anatomy tables and later popularized by Meynert (1872). Bruce (1889-1890) criticized Meynert's endorsement, calling it speculation and opinion, ungrounded in physiological fact. Bremer (1958), however, continued to advance this principle, based on the anatomical and electrophysiological research of his day (Curtis, 1940a, 1940b). As a graduate student in psychology in the late 1980s we were taught that 99% of the callosal fibers were homotopic, 1% heterotopic, with the general assumption that there is a strict topographical arrangement of axons within the corpus callosum according to origin. Frontal lobe fibers pass through the anterior section (genu), motor, somatosensory and auditory through respective midbody areas, and vision through the posterior section (splenium). The percentages may still hold true when all is said and done.

FIGURE 2. Four types of cortico-cortical projections: (1) homotopic, (2) homoareal, (3) heterotopic, and (4) ipsilateral.
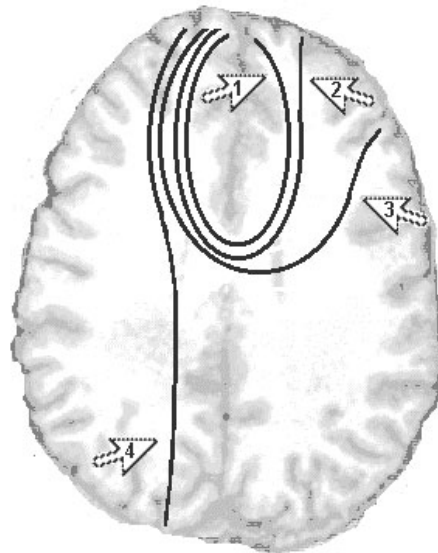
Segraves and Rosenquist (1982) examined 13 visual areas in the cat brain and reported that each area projected to and received from "a characteristic set of areas, always including the homotopic one." Yorke and Caviness (1975) found only homotopic callosal connections in the mouse. Homotopic callosal connections probably play different roles depending upon areas being linked. In areas with retinotopic representation, callosal connections are found along the vertical meridian representation area and likely serve to unify hemifield representations. Between lateralized areas, homotopic connections either are inhibitory or complementary, which may be unifying in another fashion. Clarke and Miklossy (1990) reported homoareal connections within the occipital lobe. Similar reports of homoareal connections exist for somatosensory areas in the parietal lobe and auditory areas in the temporal lobe (Kaas, 1995). Marconi, Genovesio, Giannetti, Molinari, and Caminiti (2003) studied callosal connections in dorsal premotor cortex in monkeys and identified major callosal input from the homotopic counterparts and some heterotopic connections from adjacent areas. This is a common pattern in callosal connectivity: a cortical site is connected strongly to its homologue, weakly to a few nearby sites, and ipsilaterally to the *same* nearby sites (see Figure 3). In the dorso-rostral cortex, 46% of the connections are homotopic and 49% are homoareal, spread across a few neighboring locations, rarely separated from the homologue by more than a single sulcus. For instance, in Figure 3, cortical area A could represent cortex directly below electrode F3. Neighboring ipsilateral locations 1, 2, and 3 would be nearby cortex, at most a few millimeters away, still in the frontal lobe (and probably still in medial frontal cortex). Most of their activity would also register at the same electrode (F3). The homologue, A-prime, would represent cortex below electrode F4 and 1-, 2-, and 3-prime would likewise be millimeters away, not far away from electrode F4. For comparative distances, scalp electrodes are on average 60 millimeters apart (5 to 7 cm) with the 10-20 system.

Evidence of heterotopic connections in animals and humans is growing though currently relatively slight. Some brain areas appear to be extremely divergent callosally (Clasca, Llamas, & Reinoso-Suarez, 2000; Matsunami, Kawashima, Ueki, Fujita, & Konishi, 1994). Reciprocal and non-reciprocal heterotopic callosal connections have been reported in the cat (Segraves & Rosenquist, 1982). Right medial occipital cortex projects to left angular gyrus (Clarke, 2003), and the right inferior temporal cortex projects to Wernicke's area (Di Virgilio & Clarke, 1997). Heterotopic connections, however, when they do exist, are generally less dense than homotopic ones (Miller & Vogt, 1984).

FIGURE 3. Representation of the reciprocity of callosal connections: Strong homotopic connectivity, and wherever there are heterotopic connections, there are normally ipsilateral connections to the same areas.
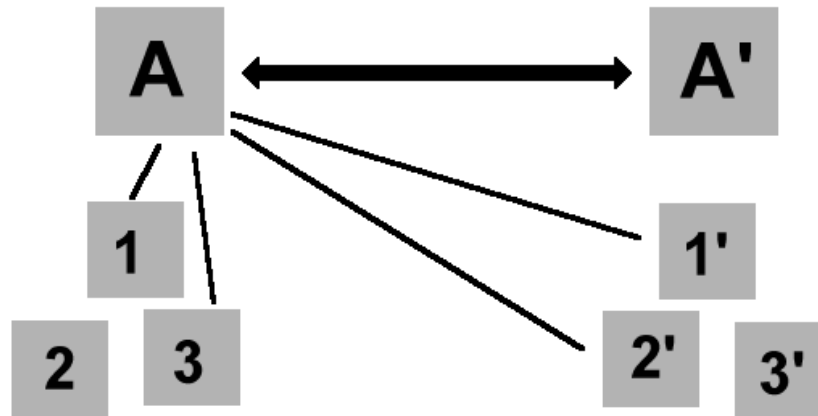
Such heterotopic connections would need to develop during ontogeny and somehow escape pruning. At birth, in all areas and species studied, callosal neurons are widely distributed, perhaps continuously throughout the cortex, including primary visual and somatosensory cortices. Transitory callosal projections are pruned during the first few weeks of life in the kitten, just prior to the period of callosal myelination (Innocenti, 1986). (Presumably the same process holds true for humans.) Seventy percent of juvenile callosal axons are eliminated in the cat and monkey (Berbel & Innocenti, 1988). The distribution is uneven after pruning, with some sections being densely connected to the other hemisphere and others only sparsely so. The overdevelopment (or exuberance) of connections, followed by specificity, is also seen in collaterals. As a juvenile the corpus callosum sports 10 branching points in the contralateral white matter (Innocenti & Bressoud, 2003) which is reduced to two in adults. In the gray matter, 500 branches compete for terminal space, leaving only 240 by adulthood. The process of neural Darwinism reduces primary visual cortex (area 17) from one of relatively abundant callosal distributions in a newborn to mostly acallosal in the adult, except at the lateral border (Lomber, Payne, & Rosenquist, 1994).

Non-callosal pathways that might also facilitate heterotopic synchrony are few and far between. The anterior commissure connects ante-

rior temporal pole, orbitofrontal cortex, and the amygdala in macaques (Pandya, Hallett, & Kmukherjee, 1969) and inferior temporal cortex, occipital cortex, and a spotty patchwork of sites in the parietal and frontal lobe in humans (Di Virgilio, Clarke, Pizzolato, & Schaffner, 1999). Besides being small, it boasts a sevenfold variation in humans (Demeter, Ringo, & Doty, 1988), so if it contributed significantly to heterotopic synchrony, we would have difficulty identifying normative synchrony patterns at these locations, which we do not (Sterman & Kaiser, 2001). Subcortical commissures (e.g., collicular) are also unlikely candidates for heterotopic synchrony as they appear to be generally topographically organized (Tardif & Clarke, 2002) and convey only low level information compared to the forebrain commissures, such as stimulus location, line orientation, and motion but not semantic/categorical information (Corballis, 1998; Tardif & Clarke, 2002).

   A plausible model for significant heterotopic contributions to EEG rhythms has yet to be developed. Such a model will need to establish a monosynaptic connection between heterotopic sites and demonstrate how the robust ipsilateral and homotopic connections are neutralized by what will presumably be slender heterotopic pathways. Electrophysiological studies are useful in verifying homotopic connections but not very helpful in establishing heterotopic ones. Until a reasonably comprehensive survey of callosal trajectories is performed, which may require significant improvements in pathway tracing technologies, we should be cautious in stray away from the general principle of homotopy. With this in mind, EEG analysis should be limited to homotopic and ipsilateral site-pairs *whenever possible*. This does not mean to reject heterotopic findings when they occur, but to seek out feasible explanations for such findings. Could such a finding be the result of an active reference? Could an interpretation relying solely on ipsilateral and homotopic synchrony be more parsimonious? We must exercise caution and not presume equipotentiality for all electrode pairings. Given the scarcity of cortical connections between, say, sites F3 and P4, or F3 and T4, or even T3 and T6, or any of the other 56 non-homotopic contralateral pairings, shared (or unshared) activity between such pairs of sites might be interpreted as a conjunction of two component pathways, the activity of each pathway alone somehow eluding our threshold of detection or analysis. The brain is the most complex object in nature, assuredly so, but it is probably more functionally complicated than it is physically complex. So what we know about its structure can guide us in interpreting its behavior.

CONCLUSIONS:
PRACTICAL IMPLICATIONS
FOR NEUROFEEDBACK PRACTITIONERS

Given what we know about hemispheric connectivity, interhemispheric training should generally be between homotopic locations (e.g., F3-F4, T3-T4). (Intrahemispheric training continues to have an equipotential appeal to it, with all electrode site pairings seeming feasible.) Even when activity at a heterotopic pairing (e.g., F3-P4) deviates from a comodulation or coherence norm, we cannot know whether the left ipsilateral, posterior homologue (F3-P3/P3-P4) circuit is the cause of the abnormal behavior, or the right ipsilateral, anterior homologue (F3-F4/F4-P4) circuit is to blame. Placing electrodes at F3 and P4 for bipolar training might drive the wrong circuit, the healthier one, and have less impact than expected on the less functional areas. (Given the complexity of the brain, perhaps all four sites could form a quadrangle of connectivity and such electrode placement would be warranted, but this should be a later step in training, after separate homologue training and intrahemispheric training fall short.) Finally, the homotopic organization of the brain gives us another training strategy to work with altogether, a somewhat non-intuitive one. A seizure focus below electrode T5, for example, can be addressed directly, with an electrode placed over the exact cortical tissue, or nearby, over healthier tissue; but the compromised site might also be addressed by strengthening (training) its homologue at T6. Cortical homologues may play a larger role in governing behavior of a site than adjoining areas. Like armies, brain areas may also be vulnerable at their flanks.

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