

Interregional synchrony of visuomotor tracking: perturbation effects
and individual differences

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Abstract

The present study evaluated the neural and behavioural correlates associated with a visuomotor tracking task during which a sensory perturbation was introduced that created a directional bias between moving hand and cursor position. The results revealed that trajectory error increased as a result of the perturbation in conjunction with a dynamic neural reorganization of cluster patterns that reflected distinct processing. In particular, a negatively activated cluster, characterizing the degraded information processing due to the perturbation, involved both hemispheres as well as midline area. Conversely, a positively activated cluster, indicative of compensatory processing was strongly confined to the left (dominant) hemisphere. In addition, a brain-behavioural association of good vs. poor performing participants enabled to localize a neural circuit within the left hemisphere and midline area that linked with successful performance. Overall, these data reinforce the functional significance of interregional synchrony in defining response output and behavioural success.

1. Introduction

Visually guided actions are intricate tasks that activate a bilateral neural network, associated with functions such as visuomotor integration, monitoring and attention [1-4]. Furthermore, they require transformations between coordinate systems in order to integrate the sensory information within the frame of reference that programs the movement [5]. Under normal conditions, visual and proprioceptive signals are compatible, usually resulting in an efficient performance. However, when the visuo-proprioceptive alignment is modified for example due to a sensory perturbation, the reference frames no longer operate in concert, and an inappropriate transformation results in a disrupted output with errors, at least initially [6-8]. In this respect, previous studies have shown that perturbed behaviour caused by sensory rotations or displaced vision, activates a widespread neural network including prefrontal, premotor, sensorimotor and parietal areas [9-12]. This line of work has revealed that brain regions play distinct roles in situations of distortion. In particular, some may be the site of perturbed processing whereas others act upon planning and/or attentional mechanisms. In response to distorted input, it is assumed that two types of processes occur as established from prism manipulation studies: (1) a recalibration process that operates until sensory input and motor output are compatible again, and (2) a strategic process that facilitates the implementation of movement corrections [8].

Even though previous research has established that various and widespread brain areas are activated by sensory perturbations, little is known about the interregional interactions that mediate information processing during perturbed conditions and how individual differences in neural connectivity profiles relate to differentiation in behaviour, i.e., success of performance. To approach this topic, the present study evaluates the neural and behavioural correlates of a visually guided tracking task during which a sensory perturbation is implemented that creates a directional bias between moving hand and cursor position. This particular situation induces a sensorimotor disturbance that imposes deviations from the intended trajectory such that updating of the visuomotor plan is necessary for reducing performance error. To evaluate the impact of the sensory perturbation as a function of

movement progress, the distortion is introduced during the first half, second half, or entire trajectory. Furthermore, the participants will be asked to report on the degree of deviation in order to compare the actual (imposed) and subjective (experienced) perturbation. This contrast enables to determine awareness of motor execution details [13]. For assessment of the neural dynamics, the data analysis of this study focuses on EEG phase synchronization, which expresses functional communication between distributed brain areas. The argument is made that the interregional connectivity profiles in the perturbed as compared to unperturbed (control) condition associate with adaptive control in order to maintain the complex task requirements.

2. Methods

2.1. Subjects

Sixteen right-handed participants (eleven female, five male, age: 28.5 ± 7.9 years) as determined by the Edinburgh handedness inventory [14] took part in the experiment. In accordance with the declaration of Helsinki, all gave informed consent to participate in the study, which was approved by the local ethics committee. Data from one participant included an excessive degree of EEG artefacts and was accordingly excluded from analysis.

2.2. Task and procedure

The participants were asked to perform a visually guided tracking task with their right hand using an ink- and wireless pen on a Wacom digitizing tablet that was attached to a PC. Task performance involved the wrist and elbow joint. The run of a trial is illustrated in Fig. 1. Each trial started with a fixation cross at either the centre of the vertically-positioned screen or at the target location of the previous trial (representing baseline). After 2000 ms, the fixation cross was replaced by a trackball that moved for 3000 ms with a speed of 2.91° visual angle/s according to a linear path towards a target position. Participants were asked to track the ball with a pen-controlled cursor as closely as possible. After 3000 ms, the trackball disappeared and a fixation cross emerged until the participant had positioned the cursor on

the target location for at least 500 ms, followed by an intertrial interval of 769 ± 395 ms during which recorded data was saved to hard disk whilst neither fixation cross nor cursor were shown.

To assess the effect of sensorimotor incongruence, a rotational perturbation was integrated that introduced a directional bias around the tracking hand. The perturbation of 60° (clockwise or counter-clockwise) occurred during the first 1500 ms of the trajectory (perturbation condition, start), the second 1500 ms of the trajectory (perturbation condition, midway), the entire trajectory (perturbation condition, entire) or not at all (control condition). The perturbation was implemented by tracking the position of the pen on the tablet at 80 Hz such that the movement direction was altered each sampling point by 60° before the cursor position was updated. In the control condition and the unperturbed phase of the start and midway conditions, there was 0° distortion. Perturbation and control conditions were randomized across blocks, each including 10 trials (or trajectories) and repeated 8 times. For the first trial of a block, the angle of the start to target position was randomized. On every other trial, the target position was the same as the start position of the preceding trial. The 3rd, 5th, 7th and 9th trial included angles that were each 72° rotated (clockwise or counter-clockwise) compared to the preceding odd trial. For example, if the first trial included a trajectory of 20° , the 3rd, 5th, 7th and 9th would be 92° , 164° , 236° and 308° or 308° , 236° , 164° and 92° , whereas each even trial would be a copy of the preceding trial, but backwards. Short breaks were included throughout the experiment. Upon completion of each block of trials, participants expressed their subjective opinion of the level of perturbation by drawing an angle in a quarter of a circle using the digitizing tablet and pen.

Insert Fig. 1 about here

2.3. Recordings and analysis

An Electrical Geodesic Inc. 128-channel system recorded continuous EEG. The signal was amplified, sampled at 250 Hz, band-pass filtered between 0.05 and 100 Hz and vertex

referenced. Data pre-processing using BESA software (MEGIS Software GmbH, Gräfelfing, Germany) included notch-filtering at 50 Hz, controlling for artefacts (such as eye movements and EMG-related activity) and application of a virtual reference-free montage. Further analysis using the EEGLAB Matlab Toolbox [15] included segmentation of the trials into epochs that were time-locked to the start of the tracking task, comprising 2000 ms fixation time, 3000 ms task performance and 250 ms post-task performance. These were subjected to a threshold-based rejection of epochs, resulting in an average of 62 epochs per subject and condition. A wavelet analysis extracted time-frequency complex phases using two cycles at frequencies in the low beta band (13-21 Hz), based on earlier work [1,16], using a sliding window of 172 ms with a frequency resolution of 0.5 Hz. A region of interest approach was adopted that focused on a restricted number of 15 electrodes, based on earlier EEG studies [1,17,18]. These were estimated to overlie prefrontal (F3, F4), premotor (FC3, FC4), sensorimotor (C3, CP3, C4, CP4), parietal (P3, P4), mesial fronto-central (Fz, FCz, Cz) including the supplementary motor area (SMA), and occipital (O1, O2) areas. Phase synchronization between these electrodes was calculated as an estimate of functional connectivity in the frequency domain. Synchronization scores were determined for all time points and averaged over 250 ms intervals for smoothing purposes with each interval overlapping 50% with the previous and the next interval. As a measurement of coupling between two signals at any given frequency, phase synchronization varies between 0 (no correlation) and 1 (perfect correlation). Before statistical comparisons were made, synchronization scores were transformed using the inverse hyperbolic tangent to stabilize variances.

The trajectories drawn on the digitizing tablet were acquired in x - and y -coordinates by using E-Prime software (Psychology Software Tools Inc., Pittsburgh, USA). The behavioural measurement was the trajectory error score defined as the RMSE over each collected time point of the smallest distance to the linear path (Fig. 1, grey area). Mean and SE are reported in the Results section.

3. Results

3.1. Visuomotor tracking: basic network

Phase synchronization in the control (unperturbed) condition was established in order to ascertain the basic network to produce the visuomotor task. To reveal the net effect of visuomotor tracking, the electrode pairs during baseline (fixation period) were compared to those during subsequent task performance. Significant positive values were retrieved that indicated involvement in performing the task. It was argued that this method would give an estimate of task-related coupling during visuomotor tracking. This calculation resulted in a widespread bilateral network (Fig. 2). Besides augmented coupling between prefrontal and sensorimotor regions, functional activation increases were observed in the midline region and various of its connections with both hemispheres. In addition, visuomotor tracking influenced activity between right frontal and occipital area as well as between interhemispheric sensorimotor and parietal regions. The mean synchronization score of the connections that comprise the basic network was 0.335 ± 0.011 . Within the left and right hemisphere couplings, synchronization scores were 0.303 ± 0.014 and 0.356 ± 0.010 , respectively.

Insert Fig. 2 about here

3.2. Perturbation effect: positive vs. negative clusters

Phase synchronization in the perturbation (entire) condition was compared to that in the control condition in order to reveal the net effect of the rotational distortion. Since this resulted in 25 statistical comparisons, a strategy was adopted based on the assumption that robustly differing electrode pairs should be significant for more than three consecutive time intervals in the same direction (negative or positive). Given independent sampling, binomial theory would predict a probability below 4% of finding more than three spuriously significant differences; a Bonferroni style approach protecting against type I errors. This computation resulted in a negative and positive cluster, distinctively characterizing the impact of the perturbation (Fig. 3). In particular, the negatively activated network was distributed and

particularly involved various connections with the occipital region, hinting at degraded processing within the areas that process visual as well as cognitive-motor information. In addition, the perturbation degraded midline-related activity, which indicates an impact on evaluative processing. In contrast, the positively activated network was localized within the left hemisphere and between centro-parietal areas of both hemispheres, suggestive of compensatory processing. The mean synchronization score of the positive cluster in the perturbation condition was 0.442 ± 0.018 , and comprised a significant increase from the control condition, $t(14)=4.07$, $p<0.01$. The mean synchronization score of the negative cluster in the perturbation condition was 0.349 ± 0.023 and involved a significant decrease from the control condition, $t(14)=-3.82$, $p<0.01$.

Insert Fig. 3 about here

Behaviourally, visuomotor tracking was degraded due to the perturbation. In particular, RMSE was larger in the perturbation than control condition, $t(14)=15.82$, $p<0.01$. The mean scores were 22.41 ± 1.34 and 6.57 ± 0.24 for the perturbation and control condition, respectively. As can be observed in Fig. 1, RMSE was largest at movement initiation and decreased as tracking progressed, indicating that subjects performed online monitoring for reducing the degree of error.

To establish the behavioural-neural relationship in the perturbation condition, the within-subject correlation coefficients between the RMSE scores and the phase synchronization scores of the positive and negative cluster networks were computed. This calculation revealed mean correlation coefficients of -0.36 (positive cluster) and -0.35 (negative cluster), $p<0.01$ for both, and points to a significant association between strength of neural activation and degree of behavioural error.

3.3. Perturbation effect: start vs. midway

The experimental design also included two conditions with a rotational perturbation at

the start and midway of the tracking action. This enabled to compare the impact of the distortion as a function of movement progress. Phase synchronization of the time interval during which the perturbation took place showed a significant difference. In particular, the start as compared to the midway perturbation involved a noticeably higher number of negative connections, primarily implicating occipital and midline regions. This observation suggests that it is neurally more efficient to cope with a perturbation when movement is in progress than when it is introduced at the start of movement. Fig. 4 depicts the dissimilarities in neural couplings between both types of perturbations.

The behavioural data revealed that RMSE was larger when the perturbation occurred at movement initiation than midway, $t(14)=3.04$, $p<0.05$. The mean scores were 17.85 ± 0.31 and 16.11 ± 0.19 for the perturbation start and midway condition, respectively.

Insert Fig. 4 about here

3.4. Individual differences: good vs. poor performing participants

To evaluate the association between the neural dynamics and individual behaviour, participants were divided into two groups based on their RMSE scores in the perturbation (entire) condition. This division resulted in a group of good performing ($n=7$) and poor performing ($n=8$) individuals. The error score in the perturbation/control condition was 2.63 ± 0.17 and 4.15 ± 1.41 for the good and poor performers, and differed significantly from one another, $t(13)=2.82$, $p<0.02$. The latter is suggestive of a greater degree of online corrective efficiency for the good vs. poor performing group. This premise was confirmed by an additional behavioural analysis that was based on the minimal Euclidean distance between the start and target position. The error score in the perturbation/control condition was 13.39 ± 1.50 and 18.14 ± 1.18 for the good and poor performers, and differed significantly from one another, $t(12)=2.53$, $p<0.03$ (complete data set from one participant were missing). Fig. 5 illustrates this behavioural dissimilarity, and suggests that the poor performers were less successful in achieving the target position than the good performers. In

other words, the achieved and required target position diverged more in the poor than good performers.

A phase synchronization analysis with respect to these groups revealed that the good as compared to the poor performing group significantly increased connectivity in a left hemisphere-midline network: F3 with FC3 and C3, midline with F3, FC3 and C3. This finding proposes that effective monitoring and planning/implementation of corrective responses are supported by a localized network.

Insert Fig. 5 about here

3.5. Awareness: Subjective reports

After completion of a block of trials, participants were asked to provide the degree of perturbation they thought had been imposed on the trajectory. The perceived perturbation differed significantly from the actual 60° perturbation as established by one sample t-tests, $t(14)=13.96$, $p<0.01$ for perturbation (entire); $t(14)=12.68$, $p<0.01$ for perturbation start; $t(14)=9.34$, $p<0.01$ for perturbation midway. The mean scores were $44.9^\circ\pm 3.2^\circ$, $43.8^\circ\pm 3.5^\circ$, and $44.6^\circ\pm 4.8^\circ$, for the perturbation entire, start, and midway condition, respectively. This result shows that the participants significantly underestimated the imposed distortion.

4. Discussion

The present work evaluated changes in functional connectivity profiles across brain regions during performance of a visuomotor tracking task. Furthermore, a sensory perturbation introduced a directional bias between moving hand and cursor position, and imposed adaptive behaviour in order to perform the task successfully. The results showed a neural reorganization of cluster patterns that reflected distinct processing. In addition, the brain-behavioural association of good vs. poor performing participants enabled to localize a neural circuit that linked with success of task execution.

Visuomotor tracking and its basic network

The visuomotor task examined in this study involved tracking of an object to a target position. It therefore involved an assignment that relied on visual and motor processes as well as on cognitive regulation to coordinate the requirements. The EEG data revealed that the visuomotor task activated a network across both hemispheres [1-4]. It is proposed that the left hemisphere facilitated the planning and execution of the tracking action, whereas the right hemisphere contributed to the interfacing of sensory information, online updating of the trajectory, and focusing of spatial attention [19-22]. Furthermore, the significance of parietal interhemispheric coupling was underscored, likely reflecting the integration of spatial and temporal information for task execution [23,24]. The findings also showed activity of the midline region and various of its connections with both hemispheres. It is argued that midline activity has crucial functions in performance evaluation as well as in motor control [25-28]. That the midline region interacted with various areas suggests widespread information transfer across organizational levels for optimal performance [22,29-33].

In addition, right frontal-occipital connectivity was observed during visuomotor tracking, suggestive of a functional loop that links cognitive and sensory processing. It likely supports a regulation mechanism that integrates information exchange between frontal and visual cortex during visually controlled movements [34]. In this respect, Fink et al. [35] argued that right prefrontal cortex monitors sensory information processed in posterior regions, and brings any incongruence to awareness. This underlines that frontal monitoring is required for detecting discrepancies between sensations when performing goal-directed actions [36].

Sensory perturbation during visuomotor tracking: Positive vs. negative cluster networks

Successful performance of a tracking task depends on the efficiency and speed of visuomotor processing. In response to perturbed input, two types of adaptive processes occur as shown from prism manipulation studies: (1) a recalibration process due to the changed spatial relation between the visual-motor and proprioceptive-motor reference frame,

and (2) a strategic process as a result of the performance disruption [8]. In agreement with this premise, the phase synchronization analysis revealed a cluster of negative and positive couplings in the perturbation relative to the control condition. The coexistence of distinct cluster activity suggests that dynamic interregional changes arise during perturbed behaviour, resulting in differentiation of processing demands.

First, the negatively activated network involved both hemispheres as well as midline area. Most noticeable was decreased connectivity of the occipital region with distributed areas. It is hypothesized that these changes characterized the degraded processing, transformation and monitoring demands of the visuomotor assignment. This finding suggests that the perturbation resulted in disintegrated information communication and extends data from Classen et al. [1] who observed reduced interregional coupling during a task that required minimizing the influence of a distracting visual stimulus. Furthermore, midline-associated activity was reduced in the perturbation condition, which points at downgraded performance evaluation. This observation is in line with recent data from a sensorimotor transformation study during which external error associated with activity in mesial frontal cortex [37].

Second, the positively activated network was strongly localized within the left hemisphere. The strengthening of these connections hints at compensatory processing to increase corrective actions, albeit assisted by motor attention [38]. In other words, the augmented activity likely reflected an intensified association between the regions involved in strategic task processing. Furthermore, the lateralization of these couplings underlines the dominance of the left hemisphere for motor control [39,40]. It is, however, noteworthy that as the visuomotor task used in this study induced visual directional errors, the participants might have adopted a strategy to minimize errors in this dimension, at least initially [41].

The experimental design also enabled to compare the impact of the sensory perturbation at the start vs. midway of the tracking action. The data showed that the start perturbation involved a noticeable higher number of negative connections than the midway perturbation, suggesting that the neural dynamics coped more efficiently when the distortion

occurred during motion in progress than when it happened at movement initiation. It implies that successive as compared to simultaneous integration of processing loads results in more effective movement regulation.

Individual differences: Brain-behaviour association

Based on the assumption that specific brain regions may be key contributors to success of performance in complex situations, an analysis was conducted to identify differences between good and poor performing participants with respect to the imposed perturbation. It was argued that such an assessment would provide insights into individual differences in behaviour in relation to brain activation. The results revealed that good performing participants (with low error scores) had increased couplings in the left hemisphere in combination with the midline area as compared to low performing participants (with high error scores). It highlights that good performing individuals augmented information processing due to the intricate task demands within the circuits that regulated monitoring and implementation of corrective actions. This between-subject observation complements within-subject data of a visuo-tactile matching task for which the magnitude of coupling between somatosensory and visual cortex correlated with behavioural success [42]. That superior output relied on an intensified distinctive circuit is a result consistent with capacity accounts of brain-behaviour associations that propose that relative processing availability underlies enhanced performance [43,44]. It further illustrates that individual activation patterns play a prominent role in this flexible regulation.

Awareness of motor performance

The experimental design further permitted a comparison between the actual (imposed) and subjective (experienced) perturbation. The data indicated that the participants significantly underestimated the scale of the perturbation, suggestive of a poor awareness of motor execution details [45]. This observation is in agreement with research that has demonstrated that participants show ineffective conscious monitoring of motor performance

[13]. Previously, it has been proposed that this regulation may be implemented within the network that is responsible for programming of the motor act [46], underlining that the experience of moving arises from a dynamic interaction between distributed areas [47]. In the present context, it is hypothesized that the perturbation-related signals were not properly identified, which might be due to inefficient sensorimotor integration in the presence of error awareness [48]. Alternatively, it is possible that the corrective actions distorted the perceived degree of perturbation or the input for conscious monitoring of the trajectory.

Conclusion. By examining functional connectivity profiles, the present data showed that multiple interconnected pathways support visually guided behaviour. When perturbed, the neural dynamics act with a reorganization of cluster patterns that represent distinctive information processing. Furthermore, brain-behavioural analysis distinguished good from poor performing participants and permitted to localize a neural circuit that associated with optimal output. Overall, these data reinforce the functional significance of interregional synchrony in defining response output and behavioural success.

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Figure Caption

Fig. 1. Schematic representation of a trial in the control and perturbation (entire) condition. After a fixation cross (baseline), participants were required to track a ballpoint (grey dot) to a target position with a cursor (black dot). In the perturbation condition, the movement direction was rotated by 60° from the actual direction (a), which affected the participants' tracking behaviour (b, as indicated by the dotted line). When reaching the target position, a fixation cross appeared on the screen until the cursor was successfully moved to this position. In the control condition, no rotation of the movement direction occurred. The trajectory error (RMSE) is illustrated by the grey area. The perturbation start and midway condition (not shown) implicated the 60° perturbation during the first and second 1500 ms of the trajectory, respectively.

Fig. 2. Functional couplings of the basic network of visuomotor tracking. A widespread bilateral network was activated, known to be involved in various functions such as visuomotor integration, monitoring and attention. The montage reflects: F3, FC3, C3, CP3, P3 (left hemisphere), F4, FC4, C4, CP4, P4 (right hemisphere), Fz, FCz, Cz (mesial fronto-central), O1, O2 (occipital). Note that the distances between the electrodes are not drawn to scale. Mesial fronto-central (midline) electrodes as well as occipital electrodes are shown as a single structure in their association with the remaining electrodes.

Fig. 3. Significant positive and negative cluster patterns when exposed to the perturbation. Whereas the negatively activated network was distributed and involved various connections with the occipital region in addition to midline-related activity, the positively activated network was localized within the left hemisphere and between centro-parietal areas of both hemispheres.

Fig. 4. Significant positive and negative cluster patterns when exposed to the perturbation midway or at initiation of movement. The start perturbation involved a higher number of negative connections than the midway perturbation.

Fig. 5. Behavioural differences as a function of performing group, illustrating a greater degree of trajectory efficiency for good as compared to poor performers in the perturbation (entire) condition. A similar performance for both groups is noted in the control condition. Error bars denote SE.

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Fig. 1

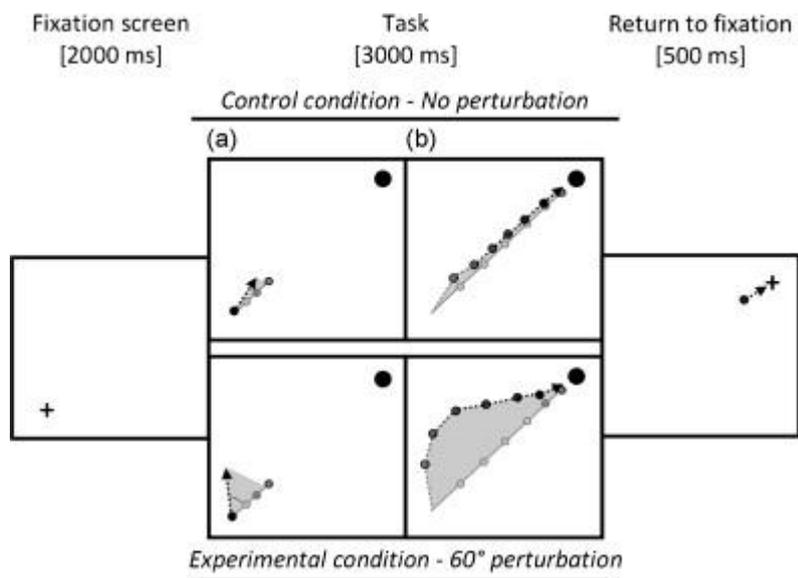


Fig. 2

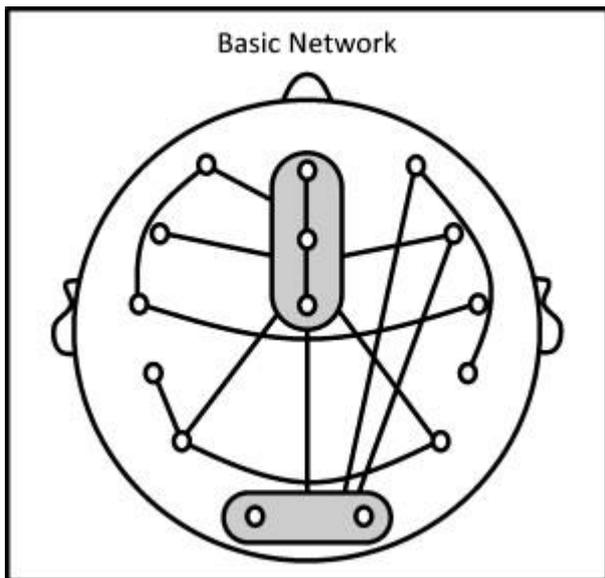


Fig. 3

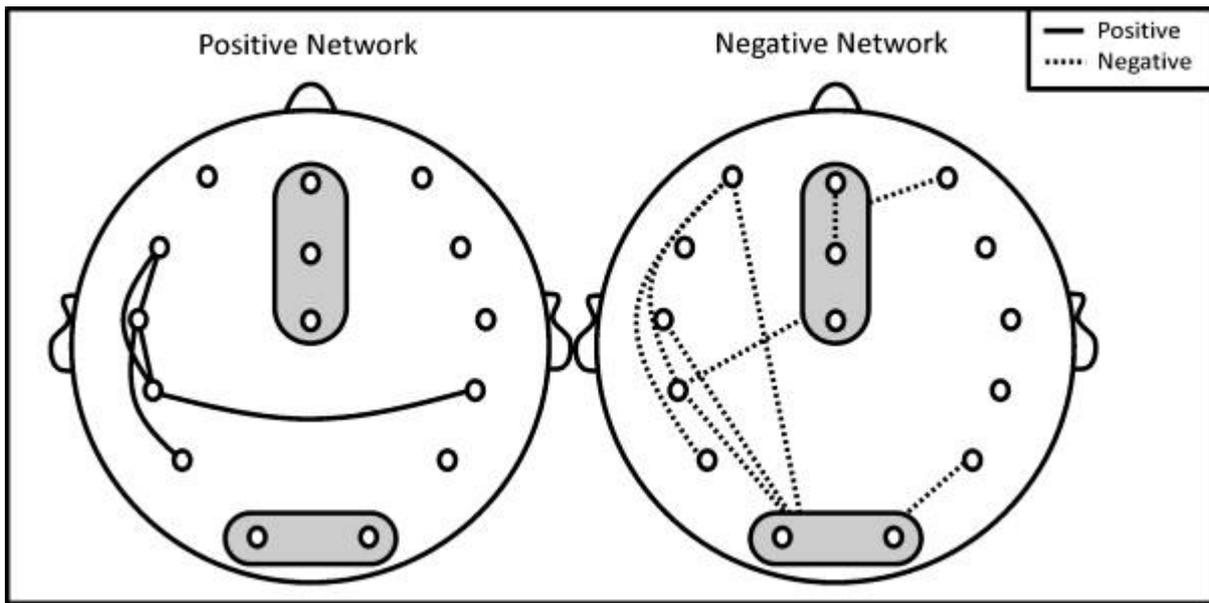


Fig. 4

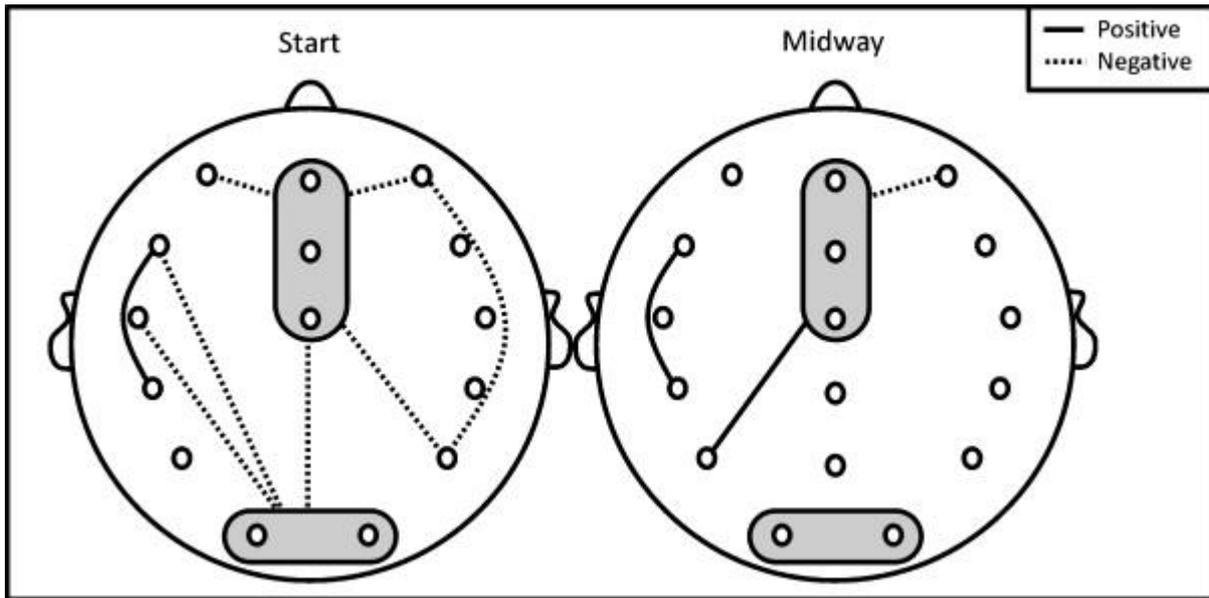


Fig. 5

