Adaptive Modification of Disparity Vergence Components: An Independent Component Analysis Study

John L. Semmlow1,2 and Weibong Yuan2

PURPOSE. Although a disparity vergence stimulus produces a smooth exponential-like response, considerable experimental evidence indicates that it is the product of at least two motor components: a pulselike transient component and a steplike sustained component. Recently, a new application of independent component analysis (ICA) has been used to decompose the vergence step response into these underlying components. Other recent experiments have shown that the vergence system is capable of rapidly modifying its dynamic characteristics (short-term adaptation) when exposed to specially designed “adapting” stimuli. Adapted responses were characterized by faster dynamics, often featuring large overshoots. In this study, ICA was used to examine changes in the underlying components produced by dynamic adaptation.

METHODS. Disparity vergence eye movements in response to identical step stimuli were obtained from four subjects both in normal (baseline) conditions and after modification by adaptive training stimuli. ICA-based component decomposition was applied to vergence step-response data sets in both normal and adapted conditions to estimate, and compare activation patterns of the two underlying components.

RESULTS. An eigenvector analysis indicated that both normal and adapted vergence responses contained two major components. ICA analysis showed that the enhanced dynamics seen in adapted responses was due to an increase in pulse component amplitude. In addition, the step component of adapted responses often showed double-step behavior in the later portion of the response. Finally, the magnitude of adaptation appeared to be related to the unadapted response dynamics.

CONCLUSIONS. The adaptive process does not evoke additional components, but modifies the two components that are present under normal conditions. Double steps seen in the step component were attributed to an interaction between pulse and step neural mechanisms. The generation of an enhanced pulse component interfered with the production of the step component. Under this scenario, the reduced initial-step component was then compensated by the generation of a second-step component, probably mediated by an internal feedback mechanism. (Invest Ophthalmol Vis Sci. 2002;43:2189–2195)

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Vergence movements, the inward or outward turning of the eyes, develop in response to several visual and psychological clues associated with depth. Under controlled-stimulus conditions, it is possible to demonstrate the influence of disparity, blur, and proximal factors on vergence position.1,2 The relative contribution of these components to a standard binocular vergence eye movement is not known precisely; however, strong evidence exists that target vergence angle, through the generation of disparity, provides the major drive to vergence eye movements,3 at least for small amplitude stimuli. This “disparity vergence” movement was originally thought to be mediated by a single control process,4–6 one that uses feedback to produce a response that results in a very small fixation error. (Vergence error, termed fixation disparity, is of the order of minutes of arc.) Although these early models provide a good general overview of disparity vergence control, considerable experimental evidence amassed in our laboratory and elsewhere indicates that responses to step changes in vergence stimulus are mediated by at least two different control processes: a pulselike or transient component and a step-like sustained component.8–10 (We use the terms pulse and step for these two components although the terms transient and sustained are also found in the literature.11,12)

Study of the control components of disparity vergence would be facilitated if there were some way to isolate them. Special brief stimulus patterns have been successful in isolating the pulse component, and this isolated component has been extensively studied and accurately modeled.13 Until recently, the step component has been much more difficult to isolate. A new technique developed in our laboratory applies independent component analysis (ICA)14–18 to multiple, or ensemble, response data to identify underlying components. Although we applied this approach only to vergence motor responses, with suitable precautions, it can be used to identify the underlying components of any response provided multiple observations of the response can be obtained. ICA has already seen numerous applications in biomedical studies including fetal electrocardiogram (ECG) extraction,19 ECG analysis,20 analysis of electroencephalogram (EEG) and magnetoencephalogram (MEG),21 optical imaging,22 and functional magnetic resonance imaging (fMRI) analysis.23–24

The conventional application of ICA recovers signals that have been mixed together (the hidden source signals), using several different measurements of the combined, observable signals, usually taken from different physical locations. (The number of observable signals must be greater than or equal to the number of hidden source signals.) In our application, each of a number of vergence responses produced by the same stimulus is treated as a separate observed signal. The approach takes advantage of the fact that underlying control components have some inherent response-to-response variability, and this variability can be used to identify component contributions to the total response.

ICA analysis requires only that the hidden signals arise from independent sources. Assuming separate neural processes generate the pulse and step components, these source signals can be taken as independent. However, they share a common
triggering stimulus, and this could result in a temporary loss of independence due to stimulus-induced synchronization. An approach that analyzed only the latter portion of the responses was developed to treat this problem and is described in the Methods section. Simulations of a two-component model of disparity vergence were used to verify to ability of ICA to identify the underlying components.

Adaptation is an important control strategy found in many motor control systems, and has been particularly well studied in saccadic eye movements. In the vergence system the level of the tonic component (also known as “dark vergence”) can be adaptively modified by changing the sustained level of vergence response over an extended period. (Because the change in vergence demand is usually achieved using prisms, this modification is also referred to as “prism adaptation.”) Recently, our group and others have demonstrated short-term adaptive modification in the dynamics of disparity vergence eye movements. Figure 1 shows an ensemble of vergence step responses to identical 4° step stimuli (i.e., test stimuli) before and after adaptive training. The adapted response behavior was observed after a training protocol in which the test stimuli were embedded among training stimuli that required a larger amplitude response. (We used the term “adapted” responses to indicate vergence responses that have undergone the training protocol, although they are generated by the same 4° step stimulus that produced the “unadapted” responses.) Examples of possible training stimuli include double steps (commonly used in saccadic adaptive experiments) or steps immediately followed by ramps. The 4° step responses shown in Figure 1B appear to be initially mis-programmed, as if to a higher-amplitude stimulus. These inappropriately large responses then undergo a midcourse correction to attain the correct final vergence position (i.e., 4°). This behavior gives rise to responses that show much larger peak velocities and greater overshoots than found in normal responses, Figure 1. It was also found that the main sequence ratio (a measure related to the first-order dynamics of a response) increased dramatically in adapted responses compared with normal responses, indicating a fundamental change in the basic response dynamics. Recent studies have confirmed that disparity vergence adaptation involves complex modification of the dynamics of the response, not just a rescaling of the desired amplitude.

**METHODS**

**Subjects and Stimulus Presentation**

Four subjects, three men and one woman, with good binocular vision were involved in the experiments. Subjects were selected who showed tolerance for the somewhat lengthy experimental sessions and the ability to produce a large number of saccade-free vergence movements under our symmetrical stimulus conditions. One subject (JS, age 56) was highly experienced and knew the goals of the experiment. The other three subjects (YC, IA, and WO, ages 25, 25, and 27) were naive to the goals of the experiment. The research followed the tenants of the Declaration of Helsinki: Informed consent of the subjects was obtained after the nature and consequences of the experiment were explained, and the experiment was approved by the institutional review boards of both Robert Wood Johnson Medical School and Rutgers University.

The stimulus was generated by a pair of oscilloscopes (P31 phosphor and a bandwidth of 20 MHz) arranged as a haploscope to present separate vertical lines to each eye. The stimulus device was calibrated by two physical targets viewed directly by the subjects. Symmetrical target movements were generated by a microcomputer to elicit convergence eye movements. The stimulus patterns used are described later.

The responses of each eye were detected by an infrared eye-movement monitor (model 6500; Skalar, Linköping, Sweden), which has a bandwidth of 200 Hz, well above the Nyquist frequency for vergence movements. Based on measurement noise, the resolution of this monitor was estimated to be approximately 3 minutes of arc. Linearity was evaluated empirically by use of a repeated series of three-point calibrations. Based on the deviation of the center-point calibration from the theoretical linear value, the experimental deviation from linearity was found to average 5% of the total movement with a maximum of 5%. Since this linearity is acceptable, the experimental trials used only a simple two-point calibration, where the calibration points covered the full response range. For the two-point calibration, the positions of each eye in response to fixed target positions were recorded immediately before and after each experimental trial. The two-point calibration data were used to recreate the two eye movements during off-line analysis. The vergence response was taken as the computed difference between the two eye movements. Aside from calibration, no signal preprocessing, such as digital filtering, was applied to the data.

Eye movements and calibrations were recorded and stored in the laboratory computer using a standard 12-bit analog-to-digital converter sampling at 200 Hz. All associated parameters such as stimulus and calibration information were saved with the individual eye-movement records. The velocity data were calculated using a two-point central difference algorithm during off-line analysis. Data analysis and display were performed on a computer (Matlab; The MathWorks, Natick, MA and Axum; Math Soft Inc., Cambridge, MA).

Although the stimulus was carefully aligned to be equal in each eye (pure vergence), saccades often occurred, particularly in the adaptive responses. The responses from each eye were examined, and those containing noticeable saccades, or other artifacts such as blinks, were eliminated from further analysis.

**FIGURE 1.** (A) An ensemble of vergence responses to a 4° step change in vergence stimulation before adaptation. (B) An ensemble of responses from the same subject to the same stimulus after exposure to approximately 30 adapting stimuli.
eliminated. Occasionally, up to half the responses would have to be eliminated, particularly in adapted responses due to the presence of saccades.

**Experimental Protocol**

Because the basic design of the adaptation experiment has been presented in recently published literature,\(^{35}\) only a brief description of the protocol is given herein. Two different visual stimulus patterns were used in the experiment. The adaptive training stimulus was a step-ramp signal—specifically, a 4° step followed immediately by a 16 deg/sec ramp. This special stimulus pattern was found to be very effective in generating adaptive changes during preliminary experiments,\(^{35}\) although other stimuli such as double steps can be used.\(^{35}\) The test stimulus was a standard 4° step change in disparity vergence. Immediately after a test stimulus presentation, two seconds of data were recorded in each eye. The 2-second period allowed for the completion of the movement while limiting the amount of data recorded and the length of the overall experiment. Responses to training stimuli were not recorded.

The data used were acquired during two to three baseline and experimental runs on each subject. The ICA analysis requires 20 to 30 clean responses, but more than twice that number were acquired to allow for the rejection of responses containing artifact or large saccades. Before an adaptive run, the responses to a series of standard step stimuli were taken as baseline data. An adaptive run consisted of three modes: adapt mode, sustain mode, and recovery mode. In the adapt mode, 50 training stimuli were randomly interspersed with 10 test stimuli. The sustain mode was similar, except that the ratio of the two stimuli was three training to one test, allowing for more rapid acquisition of adapted responses. Only the last five test stimuli in the adapt mode and those in the following sustain mode were analyzed, to ensure that these responses showed fully adapted behavior. Data taken during the recovery mode were not used in this report but have been published elsewhere.\(^{35}\)

The adaptive experiments described herein were somewhat challenging, because a fair number of saccade and artifact free responses must be acquired after adaptation, but before fatigue sets in. For this reason, the study was limited to analyzing 4° convergent step stimuli, because these are the largest vergence movements that most subjects can make without excessive saccades. Although experiments have been performed on a few subjects with the use of larger testing stimuli and adaptive protocols that diminish as well as enhance the response,\(^{35}\) we do not yet have sufficient data on enough subjects to perform an ICA analysis. Such alternative experimental protocols, including the analysis of divergent stimuli, are currently ongoing.

**Independent Component Analysis**

ICA is an analytical method that can isolate individual components from a mixture provided the components are nongaussian and sufficiently independent.\(^{11-18}\) The basic principles behind ICA are well described by Hyvärinen et al.\(^{36}\) in a readable, comprehensive book. ICA is based on a generative model: It attempts to explain how the sources (in this case the components) are mixed to generate the observed signals (\(x\)). Of course, it is desirable to use as much of the response as possible to calculate the unmixing matrix while still avoiding the initial portion where component signal independence is compromised. A rule established empirically during simulations took the point of maximum ensemble variance as the dividing line; however, the exact point was not particularly critical. This point occurred around 200 ms after the onset of the response.

In some simulation runs, an error in the initial portion of the response manifested as a negative-going step component. Because all responses were unidirectional, always convergent, the underlying components were also unidirectional. This error could be corrected by additional rotation and scaling, but this was not required for experimental data.\(^{26}\)

Another important assumption in the ICA model is that the sources are not only independent but undergo instantaneous linear mixing to produce the observed signals. Although no biological process is likely to be truly linear, extensive eye movement data indicate that separate neural signals, such as those from version and vergence neural center combine more or less linearly.

Several popular ICA algorithms are available on the Internet as script files in a computer program (Matlab; The MathWorks). In this study, we investigated two such algorithms: the FastICA algorithm developed by the ICA Group at Helsinki University (this algorithm is available at http://www.cis.hut.fi/projects/ica/fastica/fp.html) and the Jade algorithm for real-valued signals developed by Jean-Francois Cardoso (available at http://sig.enst.fr/~cardoso/stuff.html). Although the two algorithms use different approaches, they generally performed the same on both simulated and experimental data. The FastICA algorithm was selected for our current analysis, because it was found to converge somewhat more reliably than the Jade algorithm. (Such failures are usually due to inappropriate initial variables, and in those few cases in which the algorithm failed to converge correctly, it was simply rerun.)

The basic idea behind ICA starts with the equation: an assumption that the measured signals (\(x\)) are simply linear combinations of the source signals (\(s\)) plus noise. In matrix terms, the mixing represented by \(A\) can be interpreted as a rotation and a scaling of the source signals represented by \(s\). If true, then there should be some rotation and scaling that when applied to the observable signals (\(x\)) recovers the hidden source signals (\(s\)). This recovery operation is represented by an “unmixing” matrix (\(U\)) that is the inverse of \(A (U = A^{-1})\). In accordance with the fact that mixtures of independent variables have distributions that are closer to Gaussian than the unmixed signals, ICA algorithms rotate and scale the data set, using an optimization procedure to search for a result that is the least Gaussian (or some similar criterion). There are a quite a number of different approaches for estimating the unmixing matrix (\(U\)), differing primarily in the criterion that is optimized and in the optimization algorithm.\(^{18}\)

In this application, the signals produced by the neural control components of vergence eye movements constitute the latent variables (\(s\)) and the mixing matrix (\(A\)) accounts for their movement-to-movement variability. As mentioned, a critical assumption in ICA is that the source signals are statistically independent. In addition, they must have nongaussian distributions, because it is the “nongaussianity” of the data set that makes up the search criterion. Although vergence responses are certainly nongaussian, the initial portions of the underlying components may not be completely independent, because of stimulus-induced synchronization. In other words, even if the underlying neural sources are independent, their activation by a common stimulus could induce a temporary correlation between their responses. Because these responses continue, this stimulus effect diminishes so that the components become independent during the latter portion of the response.

To avoid errors associated with stimulus-induced synchronization, the evaluation of the unmixing matrix (\(U\)) was performed only on the latter portion of the responses, when source independence could be assured. The unmixing matrix that was obtained from the truncated data was then applied to the entire response (including the initial portion) to estimate the underlying motor components (\(s = UX\)). Of course, it is desirable to use as much of the response as possible to calculate the unmixing matrix while still avoiding the initial portion where component signal independence is compromised. A rule established empirically during simulations took the point of maximum ensemble variance as the dividing line; however, the exact point was not particularly critical. This point occurred around 200 ms after the onset of the response.

The algorithms used in this study were FastICA and Jade. Of these, the FastICA algorithm was the more robust. Because the FastICA algorithm has a more straightforward gradient descent procedure, it generally converged more reliably than the Jade algorithm. In addition, the FastICA algorithm was the more straightforward to use and interpret. The results presented in this paper were all obtained with the FastICA algorithm.
Because the initial variables are set randomly, convergence failures are unlikely to occur twice in a row. Both algorithms were implemented in a computer program (Windows-based Matlab; The MathWorks) and the analysis performed in only a few seconds on a 500-MHz computer.

To apply ICA to ensemble vergence response data, each 2-second response is treated as an observed signal. Example ensembles of vergence step responses in both normal and adapted conditions are shown in Figures 1A and 1B. Simulations showed that the algorithms produced more accurate results if the data sets were symmetrical, and each response was therefore modified by adding the inverted response to the end of the actual response to make the ensemble data symmetrical. Although this operation does not add any new information to the data set, it does change its statistical properties. After analysis, the inverted responses were discarded.

Previous results have shown that standard vergence step responses contain only two major components. This was confirmed and will be shown later for adapted responses; thus, the ICA algorithm was set to isolate two sources. Because of inherent ambiguities, ICA cannot determine the scale of the components; however, because the two components represent the average of the underlying control components, the sum of these components should equal the response average. Accordingly, the amplitude of the individual components was adjusted so that their sum corresponded to the ensemble average.

Model simulations were used to verify that this application of ICA was able to identify the underlying control components. Simulations were also used to develop and evaluate the algorithm to correct for errors related to stimulus-induced loss of independence. The model used for simulations contains two major sections representing the pulse and step neural processes and the signals they produce. The principal components generated by this technique are uncorrelated, and the first principal component accounts for as much variability in the data set as possible, although each succeeding component accounts for as much of the remaining variability as possible. PCA also generates a series of eigenvalues that describe how much of the data set’s variance is contained in the associated principal component. One popular method of estimating the number of significant components in a data set is to determine how many of the eigenvalues describe variance that is above the noise. This is often implemented with the aid of a plot of eigenvalue against number of components in a data set is to determine how many of the eigenvalues describe variance that is above the noise. This is often implemented with the aid of a plot of eigenvalue against number of components.

Figure 2A shows a typical ensemble of simulated disparity vergence responses. In simulations when the two components were activated more or less simultaneously, a corrective algorithm was needed to compensate for the transient loss of independence produced by stimulus synchronism mentioned earlier. The correction consisted of an additional rotation, and scaling applied only to the initial portion of the data, the portion that was not used to determine the mixing matrix. This correction algorithm was not required for real data, indicating sufficient independence exists between components in the real situation. We speculate that this independence is likely the result of a greater number of fluctuating variables in the real physiological system than represented in the model simulations. Figure 2B shows that even when correction was required, a very close match was found between simulated and estimated component responses.

**Principal Component Evaluation of the Number of Independent Components**

Several criteria exist for selecting the number of significant components in a multivariate data set. Several of these are based on principal component analysis (PCA), a technique for estimating the true dimensionality of a data set. The principal components generated by this technique are uncorrelated, and the first principal component accounts for as much variability in the data set as possible, although each succeeding component accounts for as much of the remaining variability as possible. PCA also generates a series of eigenvalues that describe how much of the data set’s variance is contained in the associated principal component. One popular method of estimating the number of significant components in a data set is to determine how many of the eigenvalues describe variance that is above the noise. This is implemented with the aid of a plot of eigenvalue against number of components.

**RESULTS**

**Number of Components**

Figure 3 (top left) shows the Scree plot obtained from simulated responses such as those in Figure 2A. The curve descends steeply and then flattens with eigenvalue numbers greater than three. This indicates that the data set contains only two uncorrelated sources, as is known to be the case with this simulated data. The remaining plots in Figure 3 show the Scree plots for the four subjects for both baseline step responses (closed circles) and adapted responses (open triangles). Because the absolute values of the eigenvalues are not of interest, the eigenvalues have been normalized so that they encompass more or less the same range. Note that all subjects showed curves similar to the one seen in the simulated data for both adapted and baseline data. The curves tended to flatten above the second eigenvalue. This indicates that both baseline and adapted responses consist primarily of two components. The
FIGURE 3. Scree plots, plots of data set eigenvalues against eigenvalue number, for the four subjects (labeled) and simulated data (top left). The simulated data are known to contain only two components and the curve flattens for eigenvalue numbers three and higher. The plots from the subject data are qualitatively similar for both the baseline (●) and adapted responses (△) indicating that these responses also contain two components. The Scree plots of baseline and adapted conditions have been normalized to have the same approximate range.

adaptation process does not evoke additional components, but modifies the existing components.

Independent Component Analysis

Figure 4 shows the component contributions found from the disparity vergence data sets for both normal (left side) and adapted (right side) conditions. Also shown are the average responses computed from the ensemble data (dashed lines). In all four subjects, the baseline results were qualitatively similar. The pulse component dominated the initial portion of the response, decaying after 600 to 800 ms, whereas the step component became active at the same time, or after a slight (60-ms) delay, and dominated the latter portion of the response. The step component showed distinctive double-step behavior.

A previous model-based analysis of adapted responses predicted the increase in pulse component amplitudes described in Table 1, but also predicted a delay between the pulse and step components in adapted responses not seen in Figure 4. The model-based analysis did not uncover the double-step behavior of the step component, because the model was not designed to generate multiple step components. From the perspective of the new ICA, it now appears that the delays predicted by the model were probably an artifact produced by a constrained model attempting to represent the double-step behavior.

The step component showed distinctive double-step behavior in two of the subjects. Double-step behavior can also be found occasionally in normal vergence responses. In an analysis of naturally occurring double responses, Alvarez et al. found response doubles occurred whenever the initial velocity response was less than 80% of a normal (i.e., single step) response. Analogous behavior has also been found in the saccadic system in the form of overlapping or double saccades. In a subsequent study, Alvarez et al. compared the timing of naturally occurring double responses with those produced by forced errors induced by external feedback. They found that naturally occurring double responses were significantly faster and concluded that they must be generated by an internal feedback mechanism. We speculate that a similar process occurred in the present study in the adapted responses of JS and YC. Specifically, the enhancement of the pulse component

Discussion

ICA-based component separation of the unadapted (i.e., baseline) vergence step response produced results similar to those reported previously. The baseline pulse component peaks in amplitude between 300 and 500 ms after the stimulus, then decays to zero after approximately 800 ms. The step component begins at either the same time as the pulse component, or after a slight delay, indicating that it experiences similar processing delays. The step component is relatively smooth and approaches the final value slowly, reaching the step level (4°) usually near the end of the 2-second record. Note that these traces represent the motor components, not the underlying neural signals; that is, they represent the neural signals after modification by the vergence plant. Because the vergence plant has been shown to be approximately first-order with a time constant of approximately 220 ms, the components shown are essentially low-pass filtered versions of the neural signals.

Table 1 shows that the amplitude of the pulse component varied across subjects as did the modification in amplitude brought about by the adaptive stimulus. A simple measure of the dynamics of the average baseline response is given in Table 1 (rightmost column) as the time constant, the time to reach 63% of the final value, not including the latent period. This time constant was evaluated directly from the average response data. Table 1 also shows that the ability of the adaptive stimulus to modify the pulse component amplitude was related to the baseline time constant. Thus, the subject with the fastest response (i.e., the lowest time constant, subject JS) also showed the greatest change in pulse component amplitude with adaptation, and visa versa. The significance of this relationship is not known and, with only four subjects, could be coincidence.

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led, in some subjects, to a reduction in the accompanying step component. This could occur if pulse component enhancement is achieved by the recruitment of neurons from a pool usually used by the step component. The resultant reduction in step component amplitude would then lead to the generation of a compensatory secondary step component, probably through the action of an internal feedback monitoring process.

### CONCLUSION

An evaluation of the eigenvalues of the data set showed that both normal and adapted responses were composed of two primary components. ICA decomposition applied to normal (unadapted) disparity vergence responses showed two underlying control components: a pulse component that dominated the initial portion of the response, but decayed to near zero after 600 to 800 ms, and a step component that was activated at the same time, or after a brief (60-ms) delay. Decomposition of adapted responses showed larger pulse component amplitudes.

### TABLE 1. Pulse Component Peak Amplitudes in Unadapted and Adapted Responses

<table>
<thead>
<tr>
<th>Subject</th>
<th>Unadapted (deg)</th>
<th>Adapted (deg)</th>
<th>Ratio*</th>
<th>Unadapted Time Constant (sec)</th>
</tr>
</thead>
<tbody>
<tr>
<td>JS</td>
<td>1.87</td>
<td>4.45</td>
<td>2.4</td>
<td>0.13</td>
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<tr>
<td>WO</td>
<td>1.75</td>
<td>3.85</td>
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<tr>
<td>YC</td>
<td>2.13</td>
<td>3.10</td>
<td>1.5</td>
<td>0.18</td>
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<tr>
<td>LA</td>
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<td>2.20</td>
<td>1.3</td>
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</tr>
<tr>
<td>Average</td>
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<td>3.40</td>
<td>1.9</td>
<td>0.17</td>
</tr>
<tr>
<td>SD</td>
<td>0.16</td>
<td>0.84</td>
<td>0.46</td>
<td>0.02</td>
</tr>
</tbody>
</table>

* Ratio of adapted to unadapted pulse component amplitudes.
titudes in all subjects, and two subjects showed double-step behavior in the step component. A possible explanation of this unexpected double-step behavior is that increasing the pulse component inhibits the production of an adequately scaled step component and a second-step component must be generated.

References