

modes of brain activity Nonlinear PCA: characterizing interactions between

Karl Friston, Jacquie Phillips, Dave Chawla and Christian Buchel

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 Nonlinear PCA: characterizing interactions
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between modes of brain activity

**Karl Friston^{*}, Jacquie Phillips, Dave Chawla and Christian Büchel
Allie School of the Maria Chelle Chelle
Allie Chelle Chelle Chelle Chelle Chelle Ch** *The Wellcome Department of Cognitive Neurology, Institute of Neurology, Queen Square, London WC1N 3BG, UK*

This paper presents a nonlinear principal component analysis (PCA) that identifies underlying sources
causing the expression of spatial modes or patterns of activity in neuroimaging time-series. The critical This paper presents a nonlinear principal component analysis (PCA) that identifies underlying sources causing the expression of spatial modes or patterns of activity in neuroimaging time-series. The critical aspect of this This paper presents a nonlinear principal component analysis (PCA) that identifies underlying sources
causing the expression of spatial modes or patterns of activity in neuroimaging time-series. The critical
aspect of this causing the expression of spatial modes or patterns of activity in neuroimaging time-series. The critical aspect of this technique is that, in relation to conventional PCA, the sources can interact to produce (second-order aspect of this technique is that, in relation to conventional PCA, the sources can interact to produce
(second-order) spatial modes that represent the modulation of one (first-order) spatial mode by another.
This nonlinear (second-order) spatial modes that represent the modulation of one (first-order) spatial mode by another.
This nonlinear PCA uses a simple neural network architecture that embodies a specific form for the
nonlinear mixing o This nonlinear PCA uses a simple neural network architecture that embodies a specific form for the nonlinear mixing of sources that cause observed data. This form is motivated by a second-order approximation to any general nonlinear mixing of sources that cause observed data. This form is motivated by a second-order approximation to any general nonlinear mixing and emphasizes interactions among pairs of sources. By introducing these nonlinea imation to any general nonlinear mixing and emphasizes interactions among paintroducing these nonlinearities principal components obtain with a unique rotation an not depend on the biologically implausible constraints adop The technique is illustrated by application to functional with a unique rotation and scaling that does to depend on the biologically implausible constraints adopted by conventional PCA.
The technique is illustrated by appl

mot depend on the biologically implausible constraints adopted by conventional PCA.
The technique is illustrated by application to functional (positron emission tomography and functional magnetic resonance imaging) imaging The technique is illustrated by application to functional (positron emission tomography and functional magnetic resonance imaging) imaging data where the ensuing first- and second-order modes can be interpreted in terms of magnetic resonance imaging) imaging data where the ensuing first- and second-order modes can be inter-
preted in terms of distributed brain systems. The interactions among sources render the expression of any
one mode cont preted in terms of distributed brain systems. The interactions among sources render the expression of any
one mode context-sensitive, where that context is established by the expression of other modes. The
examples conside one mode context-sensitive, where that context is established by the expression of other modes. The examples considered include interactions between cognitive states and time (i.e. adaptation or plasticity in PET data) and processing). in PET data) and among functionally specialized brain systems (using a fMRI study of colour and motion processing).
Keywords: functional neuroimaging; PCA; interactions; spatial modes; nonlinear unmixing; sources

1. INTRODUCTION

This paper introduces a new technique that falls under THE HEADDOCTION
This paper introduces a new technique that falls under
the heading of nonlinear principal component analysis
PCA) in the characterization of functional neuro-This paper introduces a new technique that falls under
the characterization component analysis
PCA), in the characterization of functional neuro-
naging time-series. This technique identifies the underif the heading of nonlinear principal component analysis PCA), in the characterization of functional neuro-
naging time-series. This technique identifies the under-
zing dynamics that determine the expression of spatial PCA), in the characterization of functional neuro-
naging time-series. This technique identifies the under-
zing dynamics that determine the expression of spatial maging time-series. This technique identifies the under-

ing dynamics that determine the expression of spatial

local or patterns of brain activity where, in contra-

listinction to conventional PCA, the underlying cause ing dynamics that determine the expression of spatial
addes or patterns of brain activity where, in contra-
istinction to conventional PCA, the underlying causes
an interact to produce second-order spatial modes order patterns of brain activity where, in contra-
istinction to conventional PCA, the underlying causes
an interact to produce second-order spatial modes.
these second-order modes represent the modulation of istinction to conventional PCA, the underlying causes
an interact to produce second-order spatial modes.
These second-order modes represent the modulation of
ne distributed brain system by another and provide for a an interact to produce second-order spatial modes.

These second-order modes represent the modulation of

the distributed brain system by another and provide for a

arsimonious characterization of multivariate time-series These second-order modes represent the modulation of
the distributed brain system by another and provide for a
arsimonious characterization of multivariate time-series
at embody poplinear interactions The distributed brain system by anoth
arsimonious characterization of mulater embody nonlinear interactions. **(a)** *Eigenimage analysis*

a
In Friston *et al.* (1993) we introduced voxel-based PCA eigenfunctional neuroimaging time-series to characterize (a) *Eigenimage analysis*

In Friston *et al.* (1993) we introduced voxel-based PCA

of functional neuroimaging time-series to characterize

istributed brain systems implicated in sensorimator In Friston *et al.* (1993) we introduced voxel-based PCA functional neuroimaging time-series to characterize istributed brain systems implicated in sensorimotor, exceptual or cognitive processes. These distributed If functional neuroimaging time-series to characterize
istributed brain systems implicated in sensorimotor,
erceptual or cognitive processes. These distributed
stems are identified with principal components or ejgenistributed brain systems implicated in sensorimotor,
erceptual or cognitive processes. These distributed
ystems are identified with principal components or eigen-
nages that correspond to spatial modes of coherent brain erceptual or cognitive processes. These distributed
ystems are identified with principal components or eigen-
nages that correspond to spatial modes of coherent brain
civity. This approach represents one of the simplest y stems are identified with principal components or eigen-
nages that correspond to spatial modes of coherent brain
in civity. This approach represents one of the simplest
 \overline{Q} sultivariate characterizations of functi mages that correspond to spatial modes of coherent brain
ctivity. This approach represents one of the simplest
bultivariate characterizations of functional neuroimaging
me-series and falls into the class of exploratory ana ctivity. This approach represents one of the simplest

Dultivariate characterizations of functional neuroimaging

me-series and falls into the class of exploratory analyses.

Fincipal component or eigenimage analysis gener Pultivariate characterizations of functional neuroimaging
me-series and falls into the class of exploratory analysis.
Fincipal component or eigenimage analysis generally
ses singular value decomposition (SVD) to identify me-series and falls into the class of exploratory analyses.

'rincipal component or eigenimage analysis generally

ses singular value decomposition (SVD) to identify a set

of orthogonal spatial modes that capture the greatest of orthogonal spatial modes that capture the greatest
amount of variance, expressed over time. As such, the
ensuing modes embody the most prominent aspects of the of orthogonal spatial modes that capture the greatest
amount of variance, expressed over time. As such, the
ensuing modes embody the most prominent aspects of the
variance-covariance structure of a given time-series amount of variance, expressed over time. As such, the
ensuing modes embody the most prominent aspects of the
variance-covariance structure of a given time-series.
Noting that the covariances among brain regions is ensuing modes embody the most prominent aspects of the variance-covariance structure of a given time-series.
Noting that the covariances among brain regions is equivalent to functional connectivity renders eigenimage Noting that the covariances among brain regions is analysis particularly interesting because it was among the equivalent to functional connectivity renders eigenimage
analysis particularly interesting because it was among the
first ways of addressing functional integration (i.e.
connectivity) in the human brain. Subsequently eigen analysis particularly interesting because it was among the
first ways of addressing functional integration (i.e.
connectivity) in the human brain. Subsequently eigen-
image analysis has been elaborated in a number of ways first ways of addressing functional integration (i.e.
connectivity) in the human brain. Subsequently eigen-
image analysis has been elaborated in a number of ways.
Notable among these are the application of canonical connectivity) in the human brain. Subsequently eigen-
image analysis has been elaborated in a number of ways.
Notable among these are the application of canonical
variate analysis (CVA: Friston *et al.* 1996*a*) multiimage analysis has been elaborated in a number of ways.
Notable among these are the application of canonical
variate analysis (CVA; Friston *et al.* 1996*a*), multi-
dimensional scaling (Friston *et al.* 1996*b*) and parti Notable among these are the application of canonical
variate analysis (CVA; Friston *et al.* 1996*b*), multi-
dimensional scaling (Friston *et al.* 1996*b*) and partial least
squares (PIS: McIntosh *et al.* 1996). Canonica variate analysis (CVA; Friston *et al.* 1996*a*), multi-
dimensional scaling (Friston *et al.* 1996*b*) and partial least
squares (PLS; McIntosh *et al.* 1996). Canonical variate
analysis was introduced in the context of dimensional scaling (Friston *et al.* 1996*b*) and partial least
squares (PLS; McIntosh *et al.* 1996). Canonical variate
analysis was introduced in the context of ManCova
(multiple analysis of covariance) and uses the gen squares (PLS; McIntosh *et al.* 1996). Canonical variate analysis was introduced in the context of ManCova (multiple analysis of covariance) and uses the generalized eigenvector solution to maximize the variance that can analysis was introduced in the context of ManCova
(multiple analysis of covariance) and uses the generalized
eigenvector solution to maximize the variance that can be
explained by some explanatory variables relative to err (multiple analysis of covariance) and uses the generalized
eigenvector solution to maximize the variance that can be
explained by some explanatory variables relative to error.
CVA can be thought of as an extension of eigen eigenvector solution to maximize the variance that can be explained by some explanatory variables relative to error.
CVA can be thought of as an extension of eigenimage analysis that refers explicitly to some explanatory v explained by some explanatory variables relative to error. CVA can be thought of as an extension of eigenimage
analysis that refers explicitly to some explanatory vari-
ables and allows for statistical inference. Partial least
squares is another name for SVD and can be thought of analysis that refers explicitly to some explanatory variables and allows for statistical inference. Partial least
squares is another name for SVD and can be thought of
as an eigenimage analysis of the cross covariances ables and allows for statistical inference. Partial least
squares is another name for SVD and can be thought of
as an eigenimage analysis of the cross covariances
between two sets of data. It was first applied to neurosquares is another name for SVD and can be thought of
as an eigenimage analysis of the cross covariances as an eigenimage analysis of the cross covariances
between two sets of data. It was first applied to neuro-
physiological data from different parts of the brain (the
right and left hemispheres: Friston 1995) and has been between two sets of data. It was first applied to neuro-
physiological data from different parts of the brain (the
right and left hemispheres; Friston 1995) and has been
developed to look at the relationships between imagi physiological data from different parts of the brain (the right and left hemispheres; Friston 1995) and has been
developed to look at the relationships between imaging right and left hemispheres; Friston 1995) and has been
developed to look at the relationships between imaging
time-series and explanatory variables pertaining to
experimental design and behaviour (McIntosh *et al.* 1996). time-series and explanatory variables pertaining to *Phil. Trans. R. Soc. Lond.* B (2000) **355**, 135⁻¹⁴⁶ 135 ¹³⁵ ¹³⁵ ^{02/00} The Royal Society

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36 K. Friston and others *Characterizing interactions betwee*
Eigenimage analysis has been applied widely to Eigenimage analysis has been applied widely to
ositron emission tomographic (PET) and subsequently
unctional magnetic resonance imaging (fMRI) data It Eigenimage analysis has been applied widely to
ositron emission tomographic (PET) and subsequently
inctional magnetic resonance imaging (fMRI) data. It
repertilly used as an exploratory device to characterize ositron emission tomographic (PET) and subsequently
inctional magnetic resonance imaging (fMRI) data. It
is generally used as an exploratory device to characterize
he main contributions to coherent brain activity. These inctional magnetic resonance imaging $(fMRI)$ data. It
is generally used as an exploratory device to characterize
he main contributions to coherent brain activity. These i generally used as an exploratory device to characterize
he main contributions to coherent brain activity. These
ariance components may, or may not, be related to
verimental design and recently spontaneous or endohe main contributions to coherent brain activity. These
ariance components may, or may not, be related to
xperimental design and recently spontaneous or endo-
census correlations have been observed in the motor ariance components may, or may not, be related to
xperimental design and recently spontaneous or endo-
enous correlations have been observed in the motor
action without experimental manipulation (Biswal et al. xperimental design and recently spontaneous or endo-
enous correlations have been observed in the motor
ystem without experimental manipulation (Biswal *et al.*) The end our correlations have been observed in the motor
 γ stem without experimental manipulation (Biswal *et al.*

1995). Despite its exploratory power eigenimage analysis
 γ : fundamentally limited for two reasons is estimated manipulation (Biswal *et al.* 1995). Despite its exploratory power eigenimage analysis is fundamentally limited for two reasons. First, it offers alw a linear decomposition of any set of neurophysio-

1995). Despite its exploratory power eigenimage analysis

i fundamentally limited for two reasons. First, it offers

nly a linear decomposition of any set of neurophysio-

decomposition of any set of neurophysio-Indian means all imited for two reasons. First, it offers thy a linear decomposition of any set of neurophysio-
Spical measurements, and second, the particular set of nly a linear decomposition of any set of neurophysio-
sigical measurements, and second, the particular set of
sigenimages or spatial modes obtained are uniquely
determined by constraints that are biologically implaydetermined by constraints that are biologically implau-
Leftermined by constraints that are biologically implau-
Leftermined spects of PCA represent inherent limitations \bullet igenimages or spatial modes obtained are uniquely
determined by constraints that are biologically implau-
ble. These aspects of PCA represent inherent limitations
 \bullet in the interpretability and usefulness of eigeni determined by constraints that are biologically implau-
ble. These aspects of PCA represent inherent limitations
and usefulness of eigenimage
abusis of biological time-series ble. These aspects of PCA represent the interpretability and use all properties.

In this paper, we introduce In the interpretability and usefulness of eigenimage
alysis of biological time-series.
In this paper we introduce a new technique that
colves both the problems of linearity and non-uniqueness

For all problems of biological time-series.

In this paper we introduce a new technique that

solves both the problems of linearity and non-uniqueness
 $\frac{1}{2}$ the modes This technique is a special case of poplinear In this paper we introduce a new technique that
esolves both the problems of linearity and non-uniqueness
f the modes. This technique is a special case of nonlinear
CA that is motivated by a second-order approximation to any general interactions among a small number of 'CA that is motivated by a second-order approximation

compared interactions among a small number of

cources' or 'causes' of variance in multivariate time-series.

contribution is the technique identifies a small number o In any general interactions among a small number of

Sources' or 'causes' of variance in multivariate time-series.

In brief, this technique identifies a small number of

Interaction components that explain the most varian sources' or 'causes' of variance in multivariate time-series.

n brief, this technique identifies a small number of

variance in

he observed data while allowing for high-order intern brief, this technique identifies a small number of burces or components that explain the most variance in he observed data while allowing for high-order interburces or components that explain the most variance in
he observed data while allowing for high-order inter-
cions among these sources. The sources are identified
which the sources are identified he observed data while allowing for high-order inter-
ctions among these sources. The sources are identified
abject to, and only to, the constraint that they are ortho-
one or uncorrelated. By virtue of the nonlinear inter ctions among these sources. The sources are identified
abject to, and only to, the constraint that they are ortho-
onal or uncorrelated. By virtue of the nonlinear inter-
ctions the sources are uniquely identified eschewin abject to, and only to, the constraint that they are orthoonal or uncorrelated. By virtue of the nonlinear inter-
ctions the sources are uniquely identified eschewing the
ed to refer to unnatural constraints onal or uncorrelated. By virtue of the cions the sources are uniquely identitieed to refer to unnatural constraints.

(b) *The importance of nonlinear PCA in characterizing distributed brain systems*

characterizing distributed brain systems
As noted above, the two main limitations of conven**characterizing distributed brain systems**
As noted above, the two main limitations of conven-
lonal eigenimage analysis are that the decomposition of
ny observed time-series is in terms of linearly separable As noted above, the two main limitations of conven-
lonal eigenimage analysis are that the decomposition of
ny observed time-series is in terms of linearly separable
omnoments characterized by their spatial modes and ional eigenimage analysis are that the decomposition of
ny observed time-series is in terms of linearly separable
omponents characterized by their spatial modes and
cores Second that the spatial modes are somewhat arbiny observed time-series is in terms of linearly separable
omponents characterized by their spatial modes and
cores. Second, that the spatial modes are somewhat arbi-
crily constrained to be orthogonal and account succesomponents characterized by their spatial modes and
cores. Second, that the spatial modes are somewhat arbi-
rarily constrained to be orthogonal and account, succes-
welv for the largest amount of variance. In general, the cores. Second, that the spatial modes are somewhat arbi-
rarily constrained to be orthogonal and account, succes-
vely, for the largest amount of variance. In general, the rarily constrained to be orthogonal and account, successively, for the largest amount of variance. In general, the lentification of independent components (independent amount analysis or ICA) is only possible to with ively, for the largest amount of variance. In general, the
dentification of independent components (independent
omponent analysis or ICA) is only possible to within
me permutation and scaling PCA relaxes the requirestructured independent components (independent omponent analysis or ICA) is only possible to within
the permutation and scaling. PCA relaxes the require-
ent of independence and replaces it with orthogonality ment analysis or ICA) is only possible to within
the permutation and scaling. PCA relaxes the require-
ent of independence and replaces it with orthogonality,
troducing the further problem that there is no unique integration and scaling. PCA relaxes the require-
the further problem that there is no unique
attion of the principal components. In PCA a unique rent of independence and replaces it with orthogonality,
troducing the further problem that there is no unique
potation of the principal components. In PCA, a unique
extation and permutation is obtained by requiring succes atroducing the further problem that there is no unique
action of the principal components. In PCA, a unique
action and permutation is obtained by requiring succes-
live modes to account for the greatest amount of variance in otation of the principal components. In PCA, a unique
otation and permutation is obtained by requiring succes-
Ove modes to account for the greatest amount of variance Γ otation and permutation is obtained by requiring successues ive modes to account for the greatest amount of variance

that remains once higher components have been

the smoved Scaling is constrained by ensuring the s live modes to account for the greatest amount of variance

that the remains once higher components have been

senoved. Scaling is constrained by ensuring the spatial

andes have unit sum of squares hat remains once higher comproved. Scaling is constrained
nodes have unit sum of squares.
From a highorical perspective moved. Scaling is constrained by ensuring the spatial
pdes have unit sum of squares.
From a biological perspective, the linearity constraint
a rather severe one. Because the decomposition is linear

is a rather severe one. Because the linearity constraint

is a rather severe one. Because the decomposition is linear

interactions

interactions
 $\frac{1}{2}$ and $\frac{1}{2}$ are causes of spatial From a biological perspective, the linearity constraint
a rather severe one. Because the decomposition is linear
precludes interactions among the causes of spatial
ades This is a highly unnatural restriction on the a rather severe one. Because the decomposition is linear
precludes interactions among the causes of spatial
podes. This is a highly unnatural restriction on the
positive syncessed by distributed brain systems where one precludes interactions among the causes of spatial rodes. This is a highly unnatural restriction on the civity expressed by distributed brain systems, where one vects to see substantial interactions that render the This is a highly unnatural restriction on the equively expressed by distributed brain systems, where one spects to see substantial interactions that render the expression of one mode sensitive to the expression of expressed by distributed brain systems, where one spects to see substantial interactions that render the expression of one mode sensitive to the expression of these. There are numerous examples of poplinear interxpects to see substantial interactions that render the xpression of one mode sensitive to the expression of thers. There are numerous examples of nonlinear interxpression of one mode sensitive to the expression of thers. There are numerous examples of nonlinear inter-
ctions and modulatory effects that shape the context-
ensitive nature of neuronal dynamics and brain activity. ctions and modulatory effects that shape the context-

explores both the problems of linearity and non-uniqueness

For the modes. This technique is a special case of nonlinear

CA that is motivated by a second-order approximation

PCA that is motivated by a second-order approx Perhaps the most compelling example, at a systems level,
is attentional modulation. Consider two distributed brain Perhaps the most compelling example, at a systems level,
is attentional modulation. Consider two distributed brain
systems, one subserving the processing of dynamic visual is attentional modulation. Consider two distributed brain
systems, one subserving the processing of dynamic visual
stimuli and the other responsible for a particular attenis attentional modulation. Consider two distributed brain
systems, one subserving the processing of dynamic visual
stimuli and the other responsible for a particular atten-
tional set. In the context of attending to visual systems, one subserving the processing of dynamic visual
stimuli and the other responsible for a particular atten-
tional set. In the context of attending to visual motion,
the neuronal responses in the visual system, elic stimuli and the other responsible for a particular attentional set. In the context of attending to visual motion, the neuronal responses in the visual system, elicited by motion stimuli will depend on whether the subject i tional set. In the context of attending to visual motion,
the neuronal responses in the visual system, elicited by
motion stimuli, will depend on whether the subject is
attending to this attribute or not. Attentional statu the neuronal responses in the visual system, elicited by
motion stimuli, will depend on whether the subject is
attending to this attribute or not. Attentional status will
be reflected in the activity of some attentional mo motion stimuli, will depend on whether the subject is
attending to this attribute or not. Attentional status will be reflected in the activity of some attentional mode and be reflected in the activity of some attentional mode and
therefore the expression of the visual processing mode
will be a function of the expression of the attentional
mode. It is more than likely that the implicit intera therefore the expression of the visual processing mode
will be a function of the expression of the attentional
mode. It is more than likely that the implicit interaction
between the visual and attentional modes will result will be a function of the expression of the attentional mode. It is more than likely that the implicit interaction between the visual and attentional modes will result not mode. It is more than likely that the implicit interaction
between the visual and attentional modes will result not
only in the degree to which the modes are expressed, but
in their form or relative regionally specific con between the visual and attentional modes will result not
only in the degree to which the modes are expressed, but
in their form or relative regionally specific contributions.
For example, activity in visual area V5, that h only in the degree to which the modes are expressed, but
in their form or relative regionally specific contributions.
For example, activity in visual area V5, that has been
implicated in the processing of visual motion (Ze in their form or relative regionally specific contributions.
For example, activity in visual area V5, that has been
implicated in the processing of visual motion (Zeki 1990), For example, activity in visual area V5, that has been
implicated in the processing of visual motion (Zeki 1990),
may be enhanced (relative to say V2 or V1) whenever the
appropriate attentional mode is being expressed (Tr implicated in the processing of visual motion (Zeki 1990),
may be enhanced (relative to say V2 or V1) whenever the
appropriate attentional mode is being expressed (Treue &
Maunsell 1996: Bichel *et al.* 1998) This contextmay be enhanced (relative to say V2 or V1) whenever the
appropriate attentional mode is being expressed (Treue &
Maunsell 1996; Büchel *et al.* 1998). This context-sensitive
expression of spatial modes can be modelled conc appropriate attentional mode is being expressed (Treue & Maunsell 1996; Büchel *et al.* 1998). This context-sensitive expression of spatial modes can be modelled conceptually in terms of first- and second-order effects. In Maunsell 1996; Büchel *et al.* 1998). This context-sensitive expression of spatial modes can be modelled conceptually in terms of first- and second-order effects. In this example there are two sources or causes of distrib expression of spatial modes can be modelled conceptually in terms of first- and second-order effects. In this example, there are two sources or causes of distributed
neuronal responses, namely the presence of visual motion
in the visual field and attention. Both these causes are example, there are two sources or causes of distributed
neuronal responses, namely the presence of visual motion
in the visual field and attention. Both these causes are
expressed in terms of activity in their respective s neuronal responses, namely the presence of visual motion
in the visual field and attention. Both these causes are
expressed in terms of activity in their respective spatial
modes and the interactions between these two caus in the visual field and attention. Both these causes are expressed in terms of activity in their respective spatial modes and the interactions between these two causes expressed in terms of activity in their respective spatial
modes and the interactions between these two causes
would correspond to a second-order effect that was
expressed in V_2^5 . These second-order effects can be modes and the interactions between these two causes
would correspond to a second-order effect that was
expressed in V5. These second-order effects can be
thought of as changes in the first mode that depend on would correspond to a second-order effect that was
expressed in V5. These second-order effects can be
thought of as changes in the first mode that depend on
the expression of activity in the second mode or equivaexpressed in V5. These second-order effects can be thought of as changes in the first mode that depend on the expression of activity in the second mode or equivathought of as changes in the first mode that depend on
the expression of activity in the second mode or equiva-
lently modulation of one mode that is sensitive to the
context engendered by the other the expression of activity in the seedlently modulation of one mode to
context engendered by the other.
The example considered in this ntly modulation of one mode that is sensitive to the
ntext engendered by the other.
The example considered in this paper is based on a
IRI study of visual processing that was designed to

context engendered by the other.
The example considered in this paper is based on a
fMRI study of visual processing that was designed to The example considered in this paper is based on a
fMRI study of visual processing that was designed to
address the interaction between colour and motion
processing. We had expected to demonstrate that a fMRI study of visual processing that was designed to address the interaction between colour and motion processing. We had expected to demonstrate that a 'colour' mode and 'motion' mode would interact to address the interaction between colour and motion
processing. We had expected to demonstrate that a
'colour' mode and 'motion' mode would interact to
produce a second-order mode reflecting (i) reciprocal processing. We had expected to demonstrate that a 'colour' mode and 'motion' mode would interact to produce a second-order mode reflecting (i) reciprocal interactions between extrastriate areas functionally 'colour' mode and 'motion' mode would interact to
produce a second-order mode reflecting (i) reciprocal
interactions between extrastriate areas functionally
specialized for colour and motion (ii) interactions in produce a second-order mode reflecting (i) reciprocal
interactions between extrastriate areas functionally
specialized for colour and motion, (ii) interactions in
lower visual areas mediated by convergent backwards interactions between extrastriate areas functionally
specialized for colour and motion, (ii) interactions in
lower visual areas mediated by convergent backwards
efferents or (iii) interactions in the pulvinar mediated by specialized for colour and motion, (ii) interactions in
lower visual areas mediated by convergent backwards
efferents, or (iii) interactions in the pulvinar mediated by
corticothalamic loops). Two out of three of these pre lower visual areas mediated by convergent backwards efferents, or (iii) interactions in the pulvinar mediated by corticothalamic loops). Two out of three of these predic-
tions were seen (see δ 3(b)) efferents, or (iii) interactions in the pulvinar mediated by corticothalamic loops). Two out of three of these predictions were seen (see $\S 3(b)$).

In summary, to properly model the context-sensitive tions were seen (see $\S 3(b)$).
In summary, to properly model the context-sensitive
nature of distributed but coherent brain responses, it may
be necessary to address interactions among spatial modes In summary, to properly model the context-sensitive
nature of distributed but coherent brain responses, it may
be necessary to address interactions among spatial modes
that allow for the modulation of one mode by another nature of distributed but coherent brain responses, it may
be necessary to address interactions among spatial modes
that allow for the modulation of one mode by another.
These modulatory effects are second- or high-order i be necessary to address interactions among spatial modes
that allow for the modulation of one mode by another.
These modulatory effects are second- or high-order in
nature, and, correspond to an interaction among the that allow for the modulation of one mode by another.
These modulatory effects are second- or high-order in
nature and correspond to an interaction among the
underlying causes in determining a particular pattern of These modulatory effects are second- or high-order in nature and correspond to an interaction among the underlying causes in determining a particular pattern of cortical responses. This is the principle motivation for the nature and correspond to an interaction among the underlying causes in determining a particular pattern of cortical responses. This is the principle motivation for the development and use of nonlinear forms of PCA. underlying causes in determining a particular pattern of

development and use of nonlinear forms of PCA.
This paper is divided into two sections. The first section
reviews the theoretical background to nonlinear PCA This paper is divided into two sections. The first section
reviews the theoretical background to nonlinear PCA,
first in general terms and then the specific implementa-This paper is divided into two sections. The first section
reviews the theoretical background to nonlinear PCA,
first in general terms and then the specific implementa-
tion proposed here This section includes the theoreti reviews the theoretical background to nonlinear PCA,
first in general terms and then the specific implementa-
tion proposed here. This section includes the theoretical
motivation behind the particular form of the decomposi first in general terms and then the specific implementation proposed here. This section includes the theoretical motivation behind the particular form of the decomposition employed how sources and modes are identified and tion proposed here. This section includes the theoretical
motivation behind the particular form of the decomposi-
tion employed, how sources and modes are identified and
how the ensuing modes can be interpreted. The second motivation behind the particular form of the decomposition employed, how sources and modes are identified and
how the ensuing modes can be interpreted. The second
section is an illustrative application of poplinear PCA to tion employed, how sources and modes are identified and
how the ensuing modes can be interpreted. The second
section is an illustrative application of nonlinear PCA to

he original PET study used to illustrate eigenimage analysis (Friston *et al.* 1993) and a fMRI study of visual potion and colour processing that exemplifies the modunote original PET study used to illustrate eigenimage nalysis (Friston *et al.* 1993) and a fMRI study of visual notion and colour processing that exemplifies the modu-
tion of one brain system by another nalysis (Friston *et al.* 1993) and a fM notion and colour processing that exertion of one brain system by another.

2. THEORETICAL BACKGROUND (a) *Nonlinear PCA*

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2. THEORETICAL BACKGROUND

(a) *Nonlinear PCA*

Nonlinear PCA (e.g. Kramer 1991; Softky & Kammen

91: Karbunen & Joutsensalo 1994) is a natural exten-(a) *Nonlinear PCA*

991; Karhunen & Joutsensalo 1994) is a natural exten-

991; Karhunen & Joutsensalo 1994) is a natural exten-

99. on of PCA in a sense that it aims to identify a small Sionlinear PCA (e.g. Kramer 1991; Softky & Kammen
991; Karhunen & Joutsensalo 1994) is a natural exten-
on of PCA in a sense that it aims to identify a small
umber of underlying components or sources causing 991; Karhunen & Joutsensalo 1994 is a natural extension of PCA in a sense that it aims to identify a small umber of underlying components or sources causing a on of PCA in a sense that it aims to identify a small
umber of underlying components or sources causing a
ultivariate data set that best explain the observed
ariance-covariance structure. Nonlinear PCA is itself a umber of underlying components or sources causing a

sultivariate data set that best explain the observed

structure. Nonlinear PCA is itself a

dariant of related nonlinear approaches to structural In sultivariate data set that best explain the observed
Fariance–covariance structure. Nonlinear PCA is itself a
Fariant of related nonlinear approaches to structural
Frallysis that have been nioneered over the last few analysis that have been pioneered over the last few nalysis that have been pioneered over the last few Furthermorphical and include nonlinear approaches to structural
analysis that have been pioneered over the last few
ecades. These include nonlinear factor analysis (e.g.
 Λ Conald 1984) and nonlinear partial least square In alysis that have been pioneered over the last few
decades. These include nonlinear factor analysis (e.g.
 λ CDonald 1984) and nonlinear partial least squares (e.g.
 λ Nold 1999) ecades. The
CDonald 19
Nold 1992).
Imagine the cDonald 1984) and nonlinear partial least squares (e.g.
bld 1992).
Imagine that we had *m* observations of an *n*-variate.
r example *m* scans, where each scan comprised *n* voxels

For example that we had m observations of an n -variate.

or example m scans, where each scan comprised n voxels.
 $\forall e$ can represent these data as m points in an n -dimensional Imagine that we had m observations of an *n*-variate.

or example m scans, where each scan comprised n voxels.

Ve can represent these data as m points in an n -dimensional

access In conventional PCA, the first or example m scans, where each scan comprised n voxels.
We can represent these data as m points in an n -dimensional pace. In conventional PCA, the first principal compo-We can represent these data as m points in an n -dimensional pace. In conventional PCA, the first principal component corresponds to the direction of a line running along as principal axis of the resulting cloud of poi axis of the methods of the first principal compo-
the corresponds to the direction of a line running along
the principal axis of the resulting cloud of points. The
irection of this line is specified by an *n*-vector that ent corresponds to the direction of a line running along
in a principal axis of the resulting cloud of points. The
irection of this line is specified by an *n*-vector that corre-
conds to the eigenimage and the projections sponds to the eigenimage and the projections of any one of this line is specified by an n -vector that corresponds to the eigenimage and the projections of any one point on to this line give the expression of this component for the observation (i.e. point) in questions of any one of this component
or the observation (i.e. point) in question. There are two
quivalent perspectives on the role that the principal axis oint on to this line give the expression of this component
or the observation (i.e. point) in question. There are two
quivalent perspectives on the role that the principal axis
express The first is that the projection of or the observation (i.e. point) in question. There are two
quivalent perspectives on the role that the principal axis
erves. The first is that the projection of the *m* points on to
ais line has the maximum dispersion or v quivalent perspectives on the role that the principal axis α :
rves. The first is that the projection of the *m* points on to
is line has the maximum dispersion or variance. In
ther words the component scores of the fir erves. The first is that the projection of the m points on to
is line has the maximum dispersion or variance. In
ther words, the component scores of the first principal
omnoment has the most variance. The other perspect is line has the maximum dispersion or variance. In
ther words, the component scores of the first principal
omponent has the most variance. The other perspective
that the average distance of any point from this line is ther words, the component scores of the first principal
omponent has the most variance. The other perspective
that the average distance of any point from this line is omponent has the most variance. The other perspective \cdot that the average distance of any point from this line is inimized in relation to all possible lines. In other words, i.e. first principal component is the pattern that the average distance of any point from this line is inimized in relation to all possible lines. In other words, i.e. first principal component is the pattern over the *n* oxels that minimizes the unexplained variance definite parameters in the pattern over the n oxels that minimizes the unexplained variance in the ata. Nonlinear PCA adopts exactly the same principles ut allows for curvilinear lines. In brief, a curve is fitted oxels that minimizes the unexplained variance in the ata. Nonlinear PCA adopts exactly the same principles ut allows for curvilinear lines. In brief, a curve is fitted a the data in n -space such that the average distanc ata. Nonlinear PCA adopts exactly the same principles
at allows for curvilinear lines. In brief, a curve is fitted
b the data in *n*-space such that the average distance of ut allows for curvilinear lines. In brief, a curve is fitted
 \sim the data in *n*-space such that the average distance of
 \sim e data points from this principal curve is minimized

formed in This heuristic description h The data in *n*-space such that the average distance of
lead a points from this principal curve is minimized
ligure 1). This heuristic description highlights the inti-
the relationship between nonlinear PCA and the ident are data points from this principal curve is minimized
figure 1). This heuristic description highlights the inti-
tate relationship between nonlinear PCA and the identi-
cation of principal curves or surfaces (Dong & McAy figure 1). This heuristic description highlights the intitiate relationship between nonlinear PCA and the identication of principal curves or surfaces (Dong $\&$ McAvoy 1996). In the case of linear PCA, the principal axes are determined analytically using the eigenvector solution of 1996). In the case of linear PCA, the principal axes are etermined analytically using the eigenvector solution of \mathbf{p} is $n \times n$ covariance matrix. In nonlinear PCA there is no losed-form solution and iterative techni etermined analytically using the eigenvector solution of
 Γ is $n \times n$ covariance matrix. In nonlinear PCA there is no

losed-form solution and iterative techniques are gener-

lly employed These iterative approaches ar ally employed. These iterative is no losed-form solution and iterative techniques are generally employed. These iterative approaches are usually best ally best and in terms of simple neural networks using gradient **Framed in terms** of simple neural networks using gradient compared in terms of simple neural networks using gradient Ily employed. These iterative approaches are usually best

and in terms of simple neural networks using gradient

accent or descent on the weights of the connections within

a network. One attractive architecture (Kramer amed in terms of simple neural networks using gradient
scent or descent on the weights of the connections within
ne network. One attractive architecture (Kramer 1991)
at has been used in this context is based on the notion scent or descent on the weights of the connections within

ie network. One attractive architecture (Kramer 1991)

in this context is based on the notion

f 'bottle-neck nodes' These architectures have five layers The network. One attractive architecture (Kramer 1991) at has been used in this context is based on the notion f 'bottle-neck nodes'. These architectures have five layers with a mirror symmetry about the middle or third la at has been used in this context is based on the notion
f 'bottle-neck nodes'. These architectures have five layers
ith a mirror symmetry about the middle or third layer.
The first and fifth layers represent inputs and out If 'bottle-neck nodes'. These architectures have five layers
ith a mirror symmetry about the middle or third layer.
The first and fifth layers represent inputs and outputs.
The middle layer has typically a very small numb The middle or third layer.

The first and fifth layers represent inputs and outputs.

The middle layer has, typically, a very small number, \tilde{J} , \tilde{J} nodes. The intermediate layers two and four have

trace number The middle layer has, typically, a very small number, \tilde{J} , \tilde{J} nodes. The intermediate layers two and four have input or input or neurons than the input or utput layers and employ some nonlinear activation funct f nodes. The intermediate layers two and four have arger numbers of nodes or neurons than the input or utput layers and employ some nonlinear activation functight in the input or utput layers and employ some nonlinear activation func-
on. The network is trained to reproduce its input at the
utputs. This simple training forces the network to learn on. The network is trained to reproduce its input at the

r Ō x (voxel 1) Ó $V_r x +$ (*b*) $f(x,y) = V_0 + V_x x + V_y y + V_{xy} x. y$ *r* \circ ∞ ৽ voxel 1 O

I
Figure 1. Schematic illustrating the idea behind nonlinear
PCA and principal curves. In this simple example there are Figure 1. Schematic illustrating the idea behind nonlinear
PCA and principal curves. In this simple example there are
only two yoxels and a series of images corresponding to points Figure 1. Schematic illustrating the idea behind nonlinear
PCA and principal curves. In this simple example there are
only two voxels and a series of images corresponding to points
with values $\{x, y\}$ in the plots. A co PCA and principal curves. In this simple example there are
only two voxels and a series of images corresponding to points
with values $\{x, y\}$ in the plots. A conventional PCA finds the
principal line or axis given by a only two voxels and a series of images corresponding to points
with values $\{x, y\}$ in the plots. A conventional PCA finds the
principal line or axis given by a linear function of *x* and *y* that
minimizes the average s with values $\{x, y\}$ in the plots. A conventional PCA finds the
principal line or axis given by a linear function of x and y that
minimizes the average squared distance (*r*) of each point from
that line (a). Nonlinear P minimizes the average squared distance (r) of each point from that line (a) . Nonlinear PCA is exactly the same but in this instance the axis is a curve given by some nonlinear function of x and y (b) .

of x and y (b) .
a nonlinear function of the inputs that best predicts the
inputs themselves, subject to the constraint that it can be is a nonlinear function of the inputs that best predicts the
inputs themselves, subject to the constraint that it can be
expressed as a function of small number. $\tilde{\tau}$ of sources a nonlinear function of the inputs that best predicts the inputs themselves, subject to the constraint that it can be expressed as a function of small number, \tilde{J} , of sources (activities of the 'bottle-neck nodes' in inputs themselves, subject to the constraint that it can be expressed as a function of small number, \tilde{J} , of sources (activities of the 'bottle-neck nodes' in the middle layer). expressed as a function of small number, \tilde{J} , of sources (activities of the 'bottle-neck nodes' in the middle layer).
The transformation from the input to the middle layer represents a projection of the data on to th (activities of the 'bottle-neck nodes' in the middle layer).
The transformation from the input to the middle layer
represents a projection of the data on to the $\tilde{\mathcal{J}}$ principal
surfaces of the data and the nonlinear The transformation from the input to the middle layer
represents a projection of the data on to the \tilde{J} principal
surfaces of the data and the nonlinear transformation
from the middle layer to the output layer define represents a projection of the data on to the \tilde{J} principal surfaces of the data and the nonlinear transformation
from the middle layer to the output layer defines the form
of these surfaces. There are some extremely surfaces of the data and the nonlinear transformation
from the middle layer to the output layer defines the form
of these surfaces. There are some extremely interesting
issues pertaining to the use of these architectures i from the middle layer to the output layer defines the form
of these surfaces. There are some extremely interesting
issues pertaining to the use of these architectures in
identifying principal components of a poplinear sort of these surfaces. There are some extremely interesting
issues pertaining to the use of these architectures in
identifying principal components of a nonlinear sort,
but we will not pursue them here. In this paper we take issues pertaining to the use of these architectures in
identifying principal components of a nonlinear sort,
but we will not pursue them here. In this paper, we take
a somewhat different approach that embodies some identifying principal components of a nonlinear sort,
but we will not pursue them here. In this paper, we take
a somewhat different approach that embodies some
explicit constraints on the form of the nonlinearities that but we will not pursue them here. In this paper, we take
a somewhat different approach that embodies some
explicit constraints on the form of the nonlinearities that
may cause biological data and develop an alternative a somewhat different approach that embodies some
explicit constraints on the form of the nonlinearities that
may cause biological data and develop an alternative
architecture that retains the two basic principles of explicit constraints on the form of the nonlinearities that may cause biological data and develop an alternative architecture that retains the two basic principles of (i) using `bottle-neck nodes', and (ii) training the

y (voxel 2)

(*a*)

network so that the output best predicts the input in a etwork so that the
east-squares sense. **(b)** *Second-order PCA*

In this subsection we will introduce a variant of (b) **Second-order PCA**
In this subsection we will introduce a variant of
onlinear PCA that uses a specific form for the assumed
onlinear mixing of sources to produce the observed In this subsection we will introduce a variant of
onlinear PCA that uses a specific form for the assumed
onlinear mixing of sources to produce the observed
responses in data. This form is predicated on interactions onlinear PCA that uses a specific form for the assumed
onlinear mixing of sources to produce the observed
esponses in data. This form is predicated on interactions
almong sources in the genesis of multivariate time-series onlinear mixing of sources to produce the observed
esponses in data. This form is predicated on interactions
mong sources in the genesis of multivariate time-series. In what follows we shall assume that an *n-*variate obsera mong sources in the genesis of multivariate time-series.

In what follows we shall assume that an *n*-variate obser-

ation is caused by a small number of \tilde{J} underlying

purces and interactions among these sources In what follows we shall assume that an *n*-variate obser-
ation is caused by a small number of \tilde{J} underlying
ources and interactions among these sources. Generally
the observation of the *i*th variate (e.g. at the burces and interactions among these sources. Generally will be some nonlinear function of the underlying sources

$$
\mathbf{I}_i(t) = f_i(\mathbf{s}(t)),\tag{1}
$$

 $y(t) = f_i(\mathbf{s}(t)),$

There $\mathbf{y}(t) = [y_1(t), \dots y_n(t)]$ is an *n*-vector function of
 $y(t) = \begin{bmatrix} y_1(t) & y_2(t) \end{bmatrix}$ is an *n*-vector function of there $\mathbf{y}(t) = [y_1(t), \dots y_n(t)]$ is an *n*-

lime. Similarly for $\mathbf{s}(t) = [s_1(t), \dots s_{\mathcal{J}}(t)]$

A second-order approximation of the ime. Similarly for $\mathbf{s}(t) = [s_1(t), \dots, s_7(t)]$. here $\mathbf{y}(t) = [y_1(t), \dots, y_n(t)]$ is an *n*-vector function of
ne. Similarly for $\mathbf{s}(t) = [s_1(t), \dots, s_f(t)]$.
A second-order approximation of the Taylor expansion
equation (1) about some expected value $\mathbf{\bar{s}}(t)$ for the

ime. Similarly for $\mathbf{s}(t) = [s_1(t), \dots s_j(t)]$.
A second-order approximation of the Taylor expansion
f equation (1) about some expected value $\mathbf{\bar{s}}(t)$ for the
surces is given by A second-order app
f equation (1) about
ources is given by

$$
y_i(t) \approx f_i(\bar{\boldsymbol{s}}) + \sum_j \frac{\partial f_i}{\partial u_j} u_j + \sum_{j,k} \frac{\partial^2 f_i}{\partial u_j \partial u_k} u_j u_k,
$$
\n(2)

where $u(t) = (s(t) - \bar{s}(t))$ is an alternative representation of
the sources. Now incorporating all *n* observations (i.e. there $u(t) = (s(t) - \bar{s}(t))$ is an alternative representation of
he sources. Now incorporating all *n* observations (i.e.
oxels) equation (2) can be expressed in matrix form in where $u(t) = (s(t) - \bar{s}(t))$ is an alternative representation of
he sources. Now incorporating all *n* observations (i.e.
oxels) equation (2) can be expressed, in matrix form, in
erms of zeroth-first- and second-order modes re he sources. Now incorporating all *n* observations (i.e.
oxels) equation (2) can be expressed, in matrix form, in
erms of zeroth-, first- and second-order modes repre-
ented by the *n*-vectors V^0 V^1 and V^2 oxels) equation (2) can be ex

:rms of zeroth-, first- and s

:nted by the *n*-vectors V^0 , V^1 : , \boldsymbol{V}^1 and $\boldsymbol{V}^2,$

$$
(t) \approx \boldsymbol{V}^0 + \sum_j u_j \boldsymbol{V}_j^1 + \sum_{j,k} u_j u_k \boldsymbol{V}_{jk}^2,
$$

here

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$$
\begin{aligned}\n\text{where} \\
\mathbf{v}^0 &= [f_1(\mathbf{\overline{s}}), \dots, f_n(\mathbf{\overline{s}})], \quad \mathbf{V}_j^1 = \left[\frac{\partial f_1}{\partial u_j}, \dots, \frac{\partial f_n}{\partial u_j}\right], \\
\mathbf{V}_j^2 &= \left[\frac{\partial^2 f_1}{\partial u_j \partial u_k}, \dots, \frac{\partial^2 f_n}{\partial u_j \partial u_k}\right].\n\end{aligned} \tag{3}
$$

 $\begin{bmatrix} j_k = \left[\frac{\partial u_j \partial u_k}{\partial u_j \partial u_k} \right] \end{bmatrix}$. (3)

The elements of the vectors V^1 correspond to the first

rder partial derivatives in equation (2) and the elements The elements of the vectors V^1 correspond to the first
rder partial derivatives in equation (2) and the elements
f the vectors V^2 correspond to the second-order derivarder partial derivatives in equation (2) and the elements f the vectors V^2 correspond to the second-order deriva-**The vectors** V^2 correspond to the second-order derivatives. V^1 and V^2 have the natural interpretation of first-
and second-order modes respectively. In other words the f the vectors V^2 correspond to the second-order deriva-
ives. V^1 and V^2 have the natural interpretation of first-
and second-order modes, respectively. In other words the
the source is expressed in terms of the s *j* ves. V^1 and V^2 have the natural interpretation of first-

¹ nd second-order modes, respectively. In other words the

¹ nd the interaction between the *i*th and *k*th modes and second-order modes, respectively. In other words the \Box interaction between the *j*th and *k*th modes In source is expressed in terms of the interaction between the *j*t
pxpressed as a spatial mode V_{jk}^2 . Equivalently, the considered a spacial case of a more general 2 of the spatial mode V_j^1
he *j*th and *k*th modes
 V_k^2 . Equation (3) can be
given that nd the interaction between the *j*th and *k*th modes
pressed as a spatial mode V_{jk}^2 . Equation (3) can be
onsidered a special case of a more general equation that spressed as a spatial mode
onsidered a special case of a n
mbodies higher-order terms:

$$
(t) \approx \boldsymbol{V}^0 + \sum_j u_j \boldsymbol{V}_j^1 + \sum_{j,k} \sigma(u_j u_k) \boldsymbol{V}_{jk}^2,
$$
 (4)

(c) is some sigmoid or squashing function that allows for ightly more general forms of interactions among sources \overline{Q} nd ensures a unique scaling for the sources $\boldsymbol{u}(t)$. ightly more general forms of interactions among sources (c) is some sigmoid or squashing function that all jghtly more general forms of interactions among Ω nd ensures a unique scaling for the sources $u(t)$.
The above gives a suitable form for a nonlinear ghtly more general forms of interactions among sources
d ensures a unique scaling for the sources $u(t)$.
The above gives a suitable form for a nonlinear decom-
sition or PCA of a multivariate data set $v(t)$. To identify

If the sources **u**(*t*).
The above gives a suitable form for a nonlinear decom-
osition or PCA of a multivariate data set $y(t)$. To identify
be values of $y(t)$ and the spatial modes it is necessary to The above gives a suitable form for a nonlinear decom-
osition or PCA of a multivariate data set $y(t)$. To identify
he values of $u(t)$ and the spatial modes it is necessary to
sume a constraint of orthogonality for the so osition or PCA of a multivariate data set $y(t)$. To identify
he values of $u(t)$ and the spatial modes it is necessary to
ssume a constraint of orthogonality for the sources. This
i.e. natural constraint in a sense that th is a natural constraint of orthogonality for the sources. This is a natural constraint in a sense that the underlying *Phil. Trans. R. Soc. Lond.* B (2000)

causes of any biological data should be independent if causes of any biological data should be independent if
they represent true causes, and as such will be ortho-
gonal. Notice that the assumption of orthogonality is a causes of any biological data should be independent if
they represent true causes, and as such will be ortho-
gonal. Notice that the assumption of orthogonality is a
weaker assumption than independence and it is this they represent true causes, and as such will be ortho-
gonal. Notice that the assumption of orthogonality is a
weaker assumption than independence and it is this
assumption that defines the algorithm described here as a gonal. Notice that the assumption of orthogonality is a weaker assumption than independence and it is this assumption that defines the algorithm described here as a weaker assumption than independence and it is this
assumption that defines the algorithm described here as a
nonlinear PCA. Had we assumed independence then the
problem would become that of poplinear independent assumption that defines the algorithm described here as a
nonlinear PCA. Had we assumed independence then the
problem would become that of nonlinear independent
component analysis (Common 1994) which would nonlinear PCA. Had we assumed independence then the
problem would become that of nonlinear independent
component analysis (Common 1994) which would
demand a different approach problem would become that of nonlinear independent
component analysis (Common 1994) which would
demand a different approach.

(c) *Neuronal architecture and identi¢cation of n i architecture and identifiend identifiend*
nonlinear components
the neuronal architecture

nonlinear components
In this section the neuronal architecture and gradient **nonlinear components**
In this section the neuronal architecture and gradient
descent scheme used to identify sources and their modes
are described. Note that equation (4) can be treated as a In this section the neuronal architecture and gradient
descent scheme used to identify sources and their modes
are described. Note that equation (4) can be treated as a
general linear model and as such if we knew the sourc descent scheme used to identify sources and their modes
are described. Note that equation (4) can be treated as a
general linear model and as such, if we knew the sources
 $u(t)$, the modes could be estimated by minimizing general linear model and as such, if we knew the sources $u(t)$, the modes could be estimated by minimizing the residuals trace $\{R\}$ in a least squares sense, where

$$
\mathbf{R} = (\mathbf{y} - \mathbf{X}\hat{\mathbf{V}})^T (\mathbf{y} - \mathbf{X}\hat{\mathbf{V}}),
$$
 (5)

and

$$
\hat{\mathbf{V}} = [\hat{\mathbf{V}}; \hat{\mathbf{V}}^1; \hat{\mathbf{V}}^2] = (\mathbf{X}^T \mathbf{X})^{-1} \mathbf{X}^T \mathbf{y},
$$

$$
\mathbf{X} = [\mathbf{1}, u_1, \dots u_k, \ \sigma(u_1 u_2), \dots \sigma(u_k u_k)].
$$

Here **1** is a column of ones and **I**, below, is the identity matrix $(\mathbf{X}^T \mathbf{X})^{-1} \mathbf{X} \mathbf{y}$ is simply the least-squares estimator

Here 1 is a column of ones and *I*, below, is the identity
matrix. $(X^T X)^{-1} X y$ is simply the least-squares estimator
of *V* given the inputs *y* and estimated sources (and their Here **1** is a column of ones and *I*, below, is the identity matrix. $(X^T X)^{-1} X y$ is simply the least-squares estimator of *V* given the inputs *y* and estimated sources (and their interactions) in *X* The problem matrix. $(\mathbf{X}^T \mathbf{X})^{-1} \mathbf{X} \mathbf{y}$ is simply the least-squares estimator
of V given the inputs \mathbf{y} and estimated sources (and their
interactions) in \mathbf{X} . The problem therefore, reduces to
identifying the of V given the inputs y and estimated sources (and their interactions) in X . The problem therefore, reduces to identifying the variates $\hat{u}(t)$ corresponding to estimates of interactions) in **X**. The problem therefore, reduces to identifying the variates $\hat{u}(t)$ corresponding to estimates of the sources, that minimize the norm of the residuals trace $\{R\}$. By noting the existence of some identifying the variates $\hat{u}(t)$ corresponding to estimates of
the sources, that minimize the norm of the residuals
trace{ R }. By noting the existence of some vector G_i where
 $V^0G = 0$ $V^1G = 1$ for $i = i$ and 0 other $V^0 G_i = 0, \quad V^1_i G_i =$ that minimize the norm of the residuals
noting the existence of some vector G_i where
 ${}^1_i G_i = 1$ for $i = j$ and 0 otherwise and
 ${}^2_i G_i$ and non-non-nultiplying equation (4) throughout $\boldsymbol{V}_{ik}^2 \boldsymbol{G}_i =$ $a_{\mathbf{G}}(\mathbf{R})$. By noting the existence of some vector \mathbf{G}_i where ${}^0\mathbf{G}_i = 0$, $\mathbf{V}_i^1 \mathbf{G}_i = 1$ for $i = j$ and 0 otherwise and ${}^2\mathbf{G}_i = 0$ then post-multiplying equation (4) throughout ${}^k\mathbf{G}_i$ give $\mathbf{V}^0 \mathbf{G}_i = 0$, $\mathbf{V}^1_i \mathbf{G}_i = 1$ for $i = j$ and 0 otherwise and $\mathbf{V}^2_{jk} \mathbf{G}_i = 0$ then post-multiplying equation (4) throughout by \mathbf{G}_i gives $\mathbf{u}_i(t) = \mathbf{y}(t) \times \mathbf{G}_i$. This means that there must $\mathbf{V}_{jk}^2 \mathbf{G}_i = 0$ then post-multiplying equation (4) throughout
by \mathbf{G}_i gives $\mathbf{u}_i(t) = \mathbf{y}(t) \times \mathbf{G}_i$. This means that there must be
a linear combination of the inputs that gives the *i*th
source One simpl by G_i gives $u_i(t) = y(t) \times G_i$. This means that there must be
a linear combination of the inputs that gives the *i*th
source. One simply has to find the linear combination of
inputs that minimizes trace{ \mathbb{R} } for a give a linear combination of the inputs that gives the *i*th source. One simply has to find the linear combination of inputs that minimizes trace $\{R\}$ for a given input $y(t)$, subject to the constraint that the sources are o source. One simply has to find the linear combination of
inputs that minimizes trace $\{R\}$ for a given input $y(t)$,
subject to the constraint that the sources are orthogonal.
These observations lead to the following simp puts that minimizes trace $\{R\}$ for a given input $y(t)$,
bject to the constraint that the sources are orthogonal.
These observations lead to the following simple neural
twork: the network has three lavers comprising inp

These observations lead to the following simple neural network: the network has three layers comprising input, These observations lead to the following simple neural
network: the network has three layers comprising input,
middle and output layers. The input and output layers
have *n* nodes and linear activation functions and can be network: the network has three layers comprising input,
middle and output layers. The input and output layers
have *n* nodes and linear activation functions and can be
imagined as wing next to each other (figure 2). The middle and output layers. The input and output layers
have *n* nodes and linear activation functions and can be
imagined as lying next to each other (figure 2). The
middle layer comprises a small $(\mathcal{I} < n)$ number of fir have *n* nodes and linear activation functions and can be imagined as lying next to each other (figure 2). The middle layer comprises a small ($\mathcal{J} < n$) number of firstimagined as lying next to each other (figure 2). The middle layer comprises a small $(\tilde{J} < n)$ number of first-
order nodes with linear activation functions that receive
inputs from all the input nodes. In addition the m middle layer comprises a small $(\mathcal{J} < n)$ number of first-
order nodes with linear activation functions that receive
inputs from all the input nodes. In addition the middle
layer, includes, $h = n(n-1)/2$, second-order, node order nodes with linear activation functions that receive
inputs from all the input nodes. In addition the middle
layer includes $p = n(n-1)/2$ second-order nodes that
receive lateral inputs from the first-order nodes. Each inputs from all the input nodes. In addition the middle layer includes $p = n(n-1)/2$ second-order nodes that receive lateral inputs from the first-order nodes. Each layer includes $p = n(n-1)/2$ second-order nodes that receive lateral inputs from the first-order nodes. Each second-order node receives two inputs that are multiplied and subject to the nonlinear function $\sigma(.)$ to provide th receive lateral inputs from the first-order nodes. Each second-order node receives two inputs that are multiplied and subject to the nonlinear function $\sigma(\cdot)$ to provide their output. The network is trained on the feedfo second-order node receives two inputs that are multiplied
and subject to the nonlinear function $\sigma(\cdot)$ to provide their
output. The network is trained on the feedforward
connection strengths from the input layer to the f and subject to the nonlinear function $\sigma(\cdot)$ to provide their
output. The network is trained on the feedforward
connection strengths from the input layer to the firstoutput. The network is trained on the feedforward
connection strengths from the input layer to the first-
order nodes of the middle layer. The weights to the *i*th
first-order node are effectively estimates of *G*. The connection strengths from the input layer to the first-order nodes of the middle layer. The weights to the *i*th first-order node are effectively estimates of G_i . The connections from all middle-layer nodes to the outpu order nodes of the middle layer. The weights to the *i*th first-order node are effectively estimates of G_i . The connections from all middle-layer nodes to the outputs are determined using the least-squares estimators of first-order node are effectively estimates of G_i . The connections from all middle-layer nodes to the outputs are determined using the least-squares estimators of the modes given the current estimate of the sources and t connections from all middle-layer nodes to the outputs
are determined using the least-squares estimators of the
modes given the current estimate of the sources and the
inputs according to equation (5). Anti-Hebbian lateral are determined using the least-squares estimators of the modes given the current estimate of the sources and the
inputs according to equation (5). Anti-Hebbian lateral
connections (Foldiak 1993) among the first-order nodes in
the middle layer ensure that the sources $\hat{\mathbf{u}}^{($ inputs according to equation (5). Anti-Hebbian lateral
connections (Foldiak 1993) among the first-order nodes in
the middle layer ensure that the sources $\hat{u}(t)$ are ortho-
gonal. These 7×7 lateral connection streng connections (Foldiak 1993) among the first-order nodes in
the middle layer ensure that the sources $\hat{\mathbf{u}}(t)$ are ortho-
gonal. These $\tilde{\mathcal{J}} \times \tilde{\mathcal{J}}$ lateral connection strengths \mathbf{L} are

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igure 2. The neural net architecture used to estimate sources igure 2. The neural net architecture used to estimate sources
nd modes. The lower half of the schematic represents the real
corld with its sources and interactions (here only two sources igure 2. The neural net architecture used to estimate sources
nd modes. The lower half of the schematic represents the real
orld with its sources and interactions (here only two sources
and the subsequent interaction are s and modes. The lower half of the schematic represents the real orld with its sources and interactions (here only two sources and \overline{S} and the subsequent interaction are shown). These sources and interactions (\overline{u} orld with its sources and interactions (here only two sources
 \overline{a} on the subsequent interaction are shown). These sources and

iteractions (\overline{u}) cause signals (\overline{y}) in the input layer (layer 1)

at here co At the subsequent interaction are shown). These sources and
iteractions (\boldsymbol{u}) cause signals (\boldsymbol{y}) in the input layer (layer 1)
at here comprises ten voxels or channels. The signals caused
w the sources are weigh teractions (u) cause signals (y) in the input layer (layer 1)
at here comprises ten voxels or channels. The signals caused
y the sources are weighted by the voxel-specific elements of
e corresponding first, or secondis the comprises ten voxels or channels. The signals caused
y the sources are weighted by the voxel-specific elements of
ine corresponding first- or second-order spatial modes (V^1 and
 V^2). Eeedforward connections (*y* the sources are weighted by the voxel-specific elements of ie corresponding first- or second-order spatial modes (V^1 and V^2). Feedforward connections (G) from the input layer to ver 2 provide an estimate of th is a corresponding first- or second-order spatial modes (V^1 and V^2). Feedforward connections (*G*) from the input layer to typer 2 provide an estimate of the sources (*u*) in layer 2. This stimation obtains by chang ^{r2}). Feedforward connections (*G*) from the input layer to tyer 2 provide an estimate of the sources (*u*) in layer 2. The stimation obtains by changing *G* to minimize the sum of unred residuals (trace(*R*³) or diffe stimation obtains by changing **G** to minimize the sum of quared residuals (trace{ R }) or differences between the stimation obtains by changing G to minimize the sum of
quared residuals (trace $\{R\}$) or differences between the
bserved signals and those predicted by the activity in layer 3.
the activity in layer 3 results from back quared residuals (trace $\{R\}$) or differences between the
bserved signals and those predicted by the activity in layer ?
he activity in layer 3 results from backwards connections
com the estimated source and interaction bserved signals and those predicted by the activity in layer 2.

The activity in layer 3 results from backwards connections

om the estimated source and interaction nodes in layer 2.

These backward connections are the est The activity in layer 3 results from backwards connections
om the estimated source and interaction nodes in layer 2.
hese backward connections are the estimates of the spatial
addes $(V^1$ and V^2) and are determined usi om the estimated source and interaction nodes in layer 2.

These backward connections are the estimates of the spatial

rodes (V^1 and V^2) and are determined using least-squares

iven the input (\bf{v}) and the curr hese backward connections are the estimates of the spatial
iodes (V^1 and V^2) and are determined using least-squares
iven the input (y) and the current estimate of the sources
 y^1 . I ateral decorrelating or antiiodes (V^1 and V^2) and are determined using least-squares
iven the input (y) and the current estimate of the sources
 u). Lateral decorrelating or anti-Hebbian connections *L*
etween the first-order modes ensure o iven the input (y) and the current estimate of the sources u). Lateral decorrelating or anti-Hebbian connections L etween the first-order modes ensure orthogonality of the $\boldsymbol{\mu}$). Lateral decorrelating or anti-Hebbian connections \boldsymbol{L}
etween the first-order modes ensure orthogonality of the
ource estimates. Note that in the absence of any interaction
as solution would correspond to a etween the first-order modes ensure orthogonality of the
purce estimates. Note that in the absence of any interaction
respond to a conventional PCA where
 $\frac{1}{n} = \frac{1}{n} - \frac{1}{n}$ $\ddot{\theta} = \text{pinv}(\mathbf{V}^1).$

 $d = \text{pinv}(V^1).$
determined at each iteration to render the off-diagonal
lements of $\text{Cov}\{\hat{\mathbf{u}}\}$ zero: elements of Cov $\{\hat{\bm{u}}\}$ zero:

$$
\mathbf{H} \cdot = \mathbf{I} - \lambda^{-1} \Lambda^{1/2} E^T. \tag{6}
$$

to the variance of the sources in the absence of decorre-**1** is a leading diagonal matrix whose elements correspond
 \bullet the variance of the sources in the absence of decorre-
 λ ing lateral connections (i.e. $\lambda = \text{diag}\{\hat{\pmb{u}}^* \hat{\pmb{u}}^*\}$ where
 $\lambda^* = \pmb{y} \times \pmb{G}$). A $\mathbf{v}^* = \mathbf{y} \times \mathbf{G}$). Λ a
 p ectors of $\hat{\mathbf{u}}^{*T} \hat{\mathbf{u}}^*$. **Fi** onnections (i.e. $\lambda = \text{diag}\{\hat{\mathbf{u}}^*^T \hat{\mathbf{u}}^*\}$ where
and E are the eigenvalues and eigen-
Estimates of the sources are given by

$$
t = yG + uL = y \times G(I - L)^{-1}.
$$
 (7)

 $\mathbf{B} = \mathbf{y} \mathbf{G} + \mathbf{u} \mathbf{L} = \mathbf{y} \times \mathbf{G} (\mathbf{I} - \mathbf{L})^{-1}$. (7)

(5) ote that substituting equation (6) into equation (7) gives
 $\frac{\partial \mathbf{w} \mathbf{G} \mathbf{v}}{\partial \mathbf{v}} \mathbf{G}^T \mathbf{u} = \lambda$ thereby ensuring orthogonality of t The coverage vector \hat{u} and $\hat{u}^T \hat{u} = \lambda$, thereby ensuring orthogonality of the lateral sources. Implementing changes in the lateral $\frac{d}{dx}$ lov $\{\hat{\mathbf{u}}\}\propto \hat{\mathbf{u}}^T\hat{\mathbf{u}} = \lambda$, thereby ensuring orthogonality of the \circ stimated sources. Implementing changes in the lateral $\hat{i}_{\text{ov}}\{\hat{u}\}\propto \hat{u}^T\hat{u} = \lambda$ thereby ensuring orthogonality of the stimated sources. Implementing changes in the lateral onnections in this way enforces orthogonality of the rejection effected by the feed-forward c stimated sources. Implementing changes in the lateral onnections in this way enforces orthogonality of the rojection effected by the feed-forward connections at achieveration \boldsymbol{I} imposes this constraint because the onnections in this way enforces orthogonality of the rojection effected by the feed-forward connections at ach iteration. *L* imposes this constraint because the flective feed-forward connections are $G(L-L)^{-1}$ Essenrojection effected by the feed-forward connections at
ach iteration. L imposes this constraint because the
ffective feed-forward connections are $G(I-L)^{-1}$. Essen-
ally the architecture is finding the rotation and scalin ach iteration. *L* imposes this constraint because the flective feed-forward connections are $G(I-L)^{-1}$. Essenally the architecture is finding the rotation and scaling, ally the architecture is finding the rotation and scaling,
hil. Trans. R. Soc. Lond. B (2000)

of some projection on to a low-dimensional orthogonal
subspace, that, enables, the interactions, among the of some projection on to a low-dimensional orthogonal
subspace that enables the interactions, among the
projected inputs that ensue to predict as much of the subspace that enables the interactions, among the projected inputs that ensue, to predict as much of the original inputs as possible. \hat{u} enters into equation (5) with projected inputs that ensue, to predict as much of the projected inputs that ensue, to predict as much of the original inputs as possible. \hat{u} enters into equation (5) with y to compute trace{ R }. The learning rule for the esti-mates of G , corresponds to gradient des original inputs as possible. \hat{u} enters into equation (5) with y to compute trace $\{R\}$. The learning rule for the estimates of G_i corresponds to gradient descent on the trace of the residuals. In practice, we u **y** to compute trace $\{R\}$. The learning rule for the estimates of G_i corresponds to gradient descent on the trace of the residuals. In practice, we use a Nelder–Mead simplex search as implemented in MATI AR (MathWork mates of G_i corresponds to gradient descent on the trace
of the residuals. In practice, we use a Nelder–Mead
simplex search as implemented in MATLAB (MathWorks
Inc. Natick MA ISA) that minimizes trace $\{R\}$ which of the residuals. In practice, we use a Nelder–Mead
simplex search as implemented in MATLAB (MathWorks
Inc., Natick, MA, USA) that minimizes trace $\{R\}$, which
is simply a function of the input **y** and the feed-forward simplex search as implemented in MATLAB (MathWorks Inc., Natick, MA, USA) that minimizes trace $\{R\}$, which is simply a function of the input y and the feed-forward connections strengths G . This neural network appear Inc., Natick, MA, USA) that minimizes trace $\{R\}$, which
is simply a function of the input y and the feed-forward
connections strengths G . This neural network appears to
be robust and usually converges within a few t is simply a function of the input y and the feed-forward connections strengths G . This neural network appears to be robust and usually converges within a few tens of iteraconnections strengths *G*. This neural network appears to be robust and usually converges within a few tens of iterations to give estimates of the underlying sources $\hat{u}(t)$ and least-square estimates of corresponding be robust and usually converges within a few tens of iterations to give estimates of the underlying sources $\hat{u}(t)$ and least-square estimates of corresponding spatial modes *V*. Figure 2 is a schematic that tries to co least-square estimates of corresponding spatial modes V .
Figure 2 is a schematic that tries to convey the simplicity of the architecture. Here the third or output layer has Figure 2 is a schematic that tries to convey the simplicity
of the architecture. Here the third or output layer has
been reflected back on to the inputs to emphasize the
symmetry between the assumed structure of causes in of the architecture. Here the third or output layer has
been reflected back on to the inputs to emphasize the
symmetry between the assumed structure of causes in the
world and the architecture used to identify them been reflected back on to the inputs to emphas
symmetry between the assumed structure of causes
world and the architecture used to identify them. world and the architecture used to identify them.
(d) *Interpreting the estimates*

Generally, in PCA, in the absence of any variance maximization^minimization criterion, there is no unique Generally, in PCA, in the absence of any variance
maximization-minimization criterion, there is no unique
rotation of the spatial modes (i.e. any linear combination
of the modes that conforms to an orthogonal rotation is maximization-minimization criterion, there is no unique
rotation of the spatial modes (i.e. any linear combination
of the modes, that conforms to an orthogonal rotation, is
as equally good as any other). The incorporation rotation of the spatial modes (i.e. any linear combination
of the modes, that conforms to an orthogonal rotation, is
as equally good as any other). The incorporation of the
interaction term into the decomposition implicit of the modes, that conforms to an orthogonal rotation, is
as equally good as any other). The incorporation of the
interaction term into the decomposition implicit in equaas equally good as any other). The incorporation of the interaction term into the decomposition implicit in equation (3) ensures a unique rotation and, furthermore, incorporation the sigmoid function in equation (4) interaction term into the decomposition implicit in equation (3) ensures a unique rotation and, furthermore, incorporating the sigmoid function in equation (4) ensures that the scaling is uniquely determined. The latter tion (3) ensures a unique rotation and, furthermore,
incorporating the sigmoid function in equation (4)
ensures that the scaling is uniquely determined. The latter
follows from the fact that there will be some optimum incorporating the sigmoid function in equation (4) ensures that the scaling is uniquely determined. The latter follows from the fact that there will be some optimum ensures that the scaling is uniquely determined. The latter follows from the fact that there will be some optimum
squashing of each interaction term to best predict the
observed data. The reason that unique solutions obtai follows from the fact that there will be some optimum
squashing of each interaction term to best predict the
observed data. The reason that unique solutions obtain in
this form of poplinear PCA is that we have assumed a squashing of each interaction term to best predict the
observed data. The reason that unique solutions obtain in
this form of nonlinear PCA is that we have assumed a
very specific form for the high-order interactions among observed data. The reason that unique solutions obtain in
this form of nonlinear PCA is that we have assumed a
very specific form for the high-order interactions among
sources in causing the data. This is based on the pair this form of nonlinear PCA is that we have assumed a
very specific form for the high-order interactions among
sources in causing the data. This is based on the pairwise
interactions between sources as modelled by the secon very specific form for the high-order interactions among
sources in causing the data. This is based on the pairwise
interactions between sources as modelled by the second
term in equation (4). The interpretation of the sou sources in causing the data. This is based on the pairwise
interactions between sources as modelled by the second
term in equation (4). The interpretation of the sources
and their modes is relatively straightforward. interactions between sources as modelled by the second

 $\sum_i = I - \lambda^{-1} \Lambda^{1/2} E^T$.
 \sum_i is a leading diagonal matrix whose elements correspond
 \sum_i is a leading diagonal matrix whose elements correspond
 \sum_i is a leading diagonal matrix whose elements correspond
 \sum_i is The observed multivariate data can be explained by a small number of \tilde{J} sources whose expressions are given by and their modes is relatively straightforward.
The observed multivariate data can be explained by a
small number of *j* sources whose expressions are given by
 \hat{u} . The values of \hat{u} _{*j*} scale the contribution of small number of $\hat{\mathbf{J}}$ sources whose expressions are given by $\hat{\mathbf{u}}$. The values of $\hat{\mathbf{u}}_j$ scale the contribution of the first-order spatial mode V_j^{\dagger} in a way that is directly analogous to conventional spatial mode V_i^1 in a way that is directly analogous to \hat{u} . The values of \hat{u}_j scale the contribution of the first-order spatial mode V_j^{\dagger} in a way that is directly analogous to conventional PCA, where \hat{u}_j would be the *j*th component score. In addition ther spatial mode V_j^1 in a way that is directly analogous to conventional PCA, where \hat{u}_j would be the *j*th component score. In addition there are second-order effects that represent interactions between pairs of sourc conventional PCA, where $\hat{\mathbf{u}}_j$ would be the *j*th component
score. In addition there are second-order effects that
represent interactions between pairs of sources $\sigma(\hat{\mathbf{u}}_j \hat{\mathbf{u}}_k)$.
These interactions are ex score. In addition there are second-order effects that
represent interactions between pairs of sources $\sigma(\hat{\mathbf{u}}_j \hat{\mathbf{u}}_k)$.
These interactions are expressed in second-order modes
corresponding to \mathbf{V}^2 . Each se represent interactions between pairs of sources $\sigma(\hat{\mathbf{u}}_i \hat{\mathbf{u}}_k)$.
These interactions are expressed in second-order modes
corresponding to V_{jk}^2 . Each second-order mode will have
a variance component that may o 2 1 These interactions are expressed in second-order modes
corresponding to V_{jk}^2 . Each second-order mode will have
a variance component that may or may not be orthogonal
to the first-order modes. Although the sources are corresponding to \mathbf{V}_{jk}^2 . Each second-order mode will have
a variance component that may or may not be orthogonal
to the first-order modes. Although the sources are ortho-
gonal there is no explicit requirement for t a variance component that may or may not be orthogonal
to the first-order modes. Although the sources are orthogonal there is no explicit requirement for the modes to be
so. The variance accounted for by each source and in to the first-order modes. Although the sources are orthogonal there is no explicit requirement for the modes to be so. The variance accounted for by each source and inter-
action is given by gonal there is no exp
so. The variance acce
action is given by

$$
|u_j| \cdot |V_j^1|
$$
 and $|\sigma(u_j u_k)| \cdot |V_{jk}^2|$, (8)
and can be used to rank the relative contributions of each

 $|u_j| \cdot |V_j^1|$ and $|\sigma(u_j u_k)| \cdot |V_{jk}^2|$, (8)
and can be used to rank the relative contributions of each
source or interaction $| \cdot |$ denotes the vector norm (i.e. and can be used to rank the relative contributions of each
source or interaction. $|\cdot|$ denotes the vector norm (i.e.
sum of squares).
The nonlinear PCA proposed here therefore decomurce or interaction. $|\cdot|$ denotes the vector norm (i.e.
m of squares).
The nonlinear PCA proposed here therefore decom-
see a multivariate data set into first, and second-order

sum of squares).
The nonlinear PCA proposed here therefore decomposes a multivariate data set into first- and second-order components that can be ascribed to a small number of underlying sources. The number of sources will be

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examples and other shaking an international contracts. enerally greater than the minimum number acquired to
count for the rank of the multivariate data. For
xample with just three voxels or channels two sources enerally greater than the minimum number acquired to
count for the rank of the multivariate data. For
xample, with just three voxels or channels, two sources
could be sufficient if the third dimension was explained count for the rank of the multivariate data. For
xample, with just three voxels or channels, two sources
vould be sufficient if the third dimension was explained
v the interaction between these two sources. Three sources xample, with just three voxels or channels, two sources

vould be sufficient if the third dimension was explained

y the interaction between these two sources. Three sources

vould be sufficient to account for a six-dimens rould be sufficient if the third dimension was explained
y the interaction between these two sources. Three sources
rould be sufficient to account for a six-dimensional data
at and so on Clearly in the analysis of function y the interaction between these two sources. Three sources

vould be sufficient to account for a six-dimensional data

et and so on. Clearly in the analysis of functional neuro-

proximity time-series an initial dimension Fould be sufficient to account for a six-dimensional data
et and so on. Clearly in the analysis of functional neuro-
naging time-series an initial dimension reduction is ext and so on. Clearly in the analysis of functional neuro-

intial dimension reduction is

applied before nonlinear PCA can be applied. For

rample taking the first 36 spatial modes of a fMRI required the series an initial dimension reduction is
acquired before nonlinear PCA can be applied. For
ample, taking the first 36 spatial modes of a fMRI
maging time-series using conventional singular value equired before nonlinear PCA can be applied. For value and the first 36 spatial modes of a fMRI naging time-series, using conventional singular value composition would in principle require only eight xample, taking the first 36 spatial modes of a fMRI naging time-series, using conventional singular value ecomposition, would, in principle, require only eight underlying sources. In this sense, nonlinear PCA represents \rightarrow parsimonious characterization of the data that captures • nderlying sources. In this sense, nonlinear PCA represents
• parsimonious characterization of the data that captures
• onlinear interactions among spatial modes or distributed
• rain systems in a comprehensive but intuit • parsimonious characterization of the data that captures
a conlinear interactions among spatial modes or distributed
rain systems in a comprehensive but intuitive fashion.
These and other issues will be demonstrated in th I onlinear interactions among spatial modes or distributed

rain systems in a comprehensive but intuitive fashion.

These and other issues will be demonstrated in the next

decision which uses real data to illustrate the t rain systems in a comprehensive but intuitive fashior
These and other issues will be demonstrated in the next
decision, which uses real data to illustrate the technique. **3. ILLUSTRATIVE EXAMPLES**

3. ILLUSTRATIVE EXAMPLES
In this section we will use a multisubject PET study of
thal fluency and a fMRI case study of visual processing 3. ILLUSTRATIVE EXAMPLES
In this section we will use a multisubject PET study of
erbal fluency and a fMRI case study of visual processing
and some aspects of In this section we will use a multisubject PET study of
erbal fluency and a fMRI case study of visual processing
billustrate the use of nonlinear PCA and some aspects of
inctional anatomy that can be addressed with this te erbal fluency and a fMRI case study of visual processing

conductional anatomy that can be addressed with this tech-

ique The PET study is used to show that a considerable For illustrate the use of nonlinear PCA and some aspects of inctional anatomy that can be addressed with this tech-
ique. The PET study is used to show that a considerable
mount of variance can be accounted for by interact inctional anatomy that can be addressed with this tech-
ique. The PET study is used to show that a considerable
mount of variance can be accounted for by interactions ique. The PET study is used to show that a considerable
mount of variance can be accounted for by interactions
mong causes of the data and is presented for comparison
with the original linear PCA characterization in Frist mount of variance can be accounted for by interactions
mong causes of the data and is presented for comparison
ith the original linear PCA characterization in Friston *et*
 $l/(1003)$. In brief, we will show that the two exp mong causes of the data and is presented for comparison
 *i*th the original linear PCA characterization in Friston *et*
 l. (1993). In brief, we will show that the two experi-

rental factors (task and time) combine to e The interpretation in Friston et *l.* (1993). In brief, we will show that the two experi-
tental factors (task and time) combine to express t . (1993). In brief, we will show that the two experi-
rental factors (task and time) combine to express
hemselves in a second-order mode that reflects time-
enemetent adaptation of task-related responses. This ental factors (task and time) combine to express
hemselves in a second-order mode that reflects time-
ependent adaptation of task-related responses. This
ffect can be construed as large-scale neuronhysiological hemselves in a second-order mode that reflects time-
ependent adaptation of task-related responses. This
ffect can be construed as large-scale neurophysiological
laticity attributable to strategic changes in cornitive ependent adaptation of task-related responses. This
ffect can be construed as large-scale neurophysiological
lasticity attributable to strategic changes in cognitive
recessing during intrinsic, relative to extrinsic, gener ffect can be construed as large-scale neurophysiological
lasticity attributable to strategic changes in cognitive
rocessing during intrinsic, relative to extrinsic, genera-
on of words. The second example, using fMRI deals lasticity attributable to strategic changes in cognitive
rocessing during intrinsic, relative to extrinsic, genera-
ion of words. The second example, using fMRI, deals
pore explicitly with the modulation of one brain syste on of words. The second example, using fMRI, deals ore explicitly with the modulation of one brain system
y another. In particular the interactions between
pecialized cortical systems that may be mediated by
perticathelemic loops y another. In partic
pecialized cortical sys-
orticothalamic loops. **(a)** *A PET study of verbal fluency*

(*i) Data acquisition, experimental design and preprocessing*
The data were obtained from five subjects scanned 12

(a) *A PET study of verbal fluency*
Data acquisition, experimental design and preprocessing
The data were obtained from five subjects scanned 12
nes (every 8 min) while performing one of two verbal The data were obtained design and preprocessing
The data were obtained from five subjects scanned 12
times (every 8 min) while performing one of two verbal
asks. Scans were obtained with a CTI PET camera (model The data were obtained from five subjects scanned 12
times (every 8 min) while performing one of two verbal
asks. Scans were obtained with a CTI PET camera (model
53R CTI Knowille TN JSA) ¹⁵O was administered imes (every 8 min) while performing one of two verbal
asks. Scans were obtained with a CTI PET camera (model
53B, CTI, Knoxville, TN, USA). ¹⁵O was administered
atravenously as radiolabelled water infused over 2 min asks. Scans were obtained with a CTI PET camera (model
153B, CTI, Knoxville, TN, USA). ¹⁵O was administered
1travenously as radiolabelled water infused over 2 min.
16tal counts per voxel during the build-up phase of radi $T_{\rm p}$ 53B, CTI, Knoxville, TN, USA). ¹⁵O was administered
atravenously as radiolabelled water infused over 2 min.
botal counts per voxel during the build-up phase of radio-
crivity served as an estimate of regional c (b) otal counts per voxel during the build-up phase of radio-

ctivity served as an estimate of regional cerebral blood

ow (rCBF). Subjects performed two tasks in alternation.

In task involved repeating a letter presente or the task involved as an estimate of regional cerebral blood

ow (rCBF). Subjects performed two tasks in alternation.

One task involved repeating a letter presented aurally, at

ne per two seconds (word shadowing). The ow (rCBF). Subjects performed two tasks in alternation.

The task involved repeating a letter presented aurally, at

ne per two seconds (word shadowing). The other was a

aced verbal fluency task, where the subjects respo In task involved repeating a letter presented aurally, at
ne per two seconds (word shadowing). The other was a
aced verbal fluency task, where the subjects responded
it a word that began with the letter presented (intrinsi ne per two seconds (word shadowing). The other was a aced verbal fluency task, where the subjects responded *i*th a word that began with the letter presented (intrinsic and generation). The data were realigned streptactica aced verbal fluency task, where the subjects responded
 $\dot{\text{u}}$ it a word that began with the letter presented (intrinsic
 vord generation). The data were realigned, stereotactically
 Ω ormalized and smoothed wit The a word that began with the letter presented (intrinsic
 α /ord generation). The data were realigned, stereotactically
 α ormalized and smoothed with a 16 mm Gaussian kernel

Friston *et al.* 1996c). The data wer ord generation). The data were realigned, stereotactically
ormalized and smoothed with a 16 mm Gaussian kernel
Friston *et al.* 1996*c*). The data were subject to a conven-
onal SPM analysis using multiple linear regressi Formalized and smoothed with a 16 mm Gaussian kernel
Friston *et al.* 1996*c*). The data were subject to a conven-
ional SPM analysis using multiple linear regression with
2 condition-specific effects five subject effects Friston *et al.* 1996*c*). The data were subject to a conven-
lonal SPM analysis using multiple linear regression with
2 condition-specific effects, five subject effects and global activity as described in Friston *et al.* (1995*^a*). Parameter 2 condition-specific effects, five subject effects and global system equipped with a head volume coil. Contiguous civity as described in Friston *et al.* (1995*a*). Parameter multislice T_2^* -weighted fMRI images (TE =

over subjects, were selected from voxels that exceeded a over subjects, were selected from voxels that exceeded a threshold of $p < 0.05$ in the ensuing SPM $\{F\}$ and subject to nonlinear PCA as described below over subjects, were selected from v
threshold of $p < 0.05$ in the ensuing S
nonlinear PCA as described below. nonlinear PCA as described below.
(ii) *Nonlinear PCA*

Nonlinear PCA
The data were reduced to an eight-dimensional
penace using SVD and entered into the nonlinear PCA (ii) *Nonlinear PCA*
The data were reduced to an eight-dimensional
subspace using SVD and entered into the nonlinear PCA
using two sources. The ability of these two sources and The data were reduced to an eight-dimensional subspace using SVD and entered into the nonlinear PCA using two sources. The ability of these two sources, and their interaction to explain the observed regional activity subspace using SVD and entered into the nonlinear PCA
using two sources. The ability of these two sources, and
their interaction, to explain the observed regional activity
is illustrated in figure 3*a*. Here an arbitrary y using two sources. The ability of these two sources, and
their interaction, to explain the observed regional activity
is illustrated in figure 3*a*. Here an arbitrary voxel (that
showing the bighest Evalue in the conventio their interaction, to explain the observed regional activity
is illustrated in figure 3*a*. Here an arbitrary voxel (that
showing the highest *F*-value in the conventional SPM
analysis) was selected from the left inferior is illustrated in figure 3*a*. Here an arbitrary voxel (that showing the highest F -value in the conventional SPM analysis) was selected from the left inferior frontal gyrus (Brodmann Area 47). The observed condition-spe showing the highest F -value in the conventional SPM analysis) was selected from the left inferior frontal gyrus
(Brodmann Area 47). The observed condition-specific
activity, over 12 scans, is shown in black and that
predicted by the two sources is shown in white The rela-(Brodmann Area 47). The observed condition-specific activity, over 12 scans, is shown in black and that predicted by the two sources is shown in white. The rela-
tive amount of variance accounted for by the two sources activity, over 12 scans, is shown in black and that
predicted by the two sources is shown in white. The rela-
tive amount of variance accounted for by the two sources
and their interaction is shown in the middle panel. It predicted by the two sources is shown in white. The relative amount of variance accounted for by the two sources
and their interaction is shown in the middle panel. It can
be seen that 88% of the total variance, over all v tive amount of variance accounted for by the two sources
and their interaction is shown in the middle panel. It can
be seen that 88% of the total variance, over all voxels
included in the analysis, can be explained by two and their interaction is shown in the middle panel. It can
be seen that 88% of the total variance, over all voxels
included in the analysis, can be explained by two sources.
The second-order mode accounts of 2.2% of be seen that 88% of the total variance, over all voxels
included in the analysis, can be explained by two sources.
The second-order mode accounts of 2.2% of this (after
removing that which can be modelled by the first-orde included in the analysis, can be explained by two sources.
The second-order mode accounts of 2.2% of this (after
removing that which can be modelled by the first-order
effects) and would have been distributed over other The second-order mode accounts of 2.2% of this (after
removing that which can be modelled by the first-order
effects) and would have been distributed over other
modes in a conventional PCA. Figure $3b$ shows this distr removing that which can be modelled by the first-order effects) and would have been distributed over other modes in a conventional PCA. Figure 3*b* shows this distrieffects) and would have been distributed over other modes in a conventional PCA. Figure $3b$ shows this distribution indicating that the fifth and sixth eigenimages, in a conventional PCA largely comprise the interaction modes in a conventional PCA. Figure $3b$ shows this distribution indicating that the fifth and sixth eigenimages, in
a conventional PCA, largely comprise the interaction
between the two modes identified by nonlinear PCA bution indicating that the fifth and sixth eigenimages,
a conventional PCA, largely comprise the interact
between the two modes identified by nonlinear PCA.
The first- and second-order modes are seen in figure a conventional PCA, largely comprise the interaction
between the two modes identified by nonlinear PCA.
The first- and second-order modes are seen in figure 4,

rocessing during intrinsic, relative to extrinsic, genera-
impropriate cognitive set. The key regions involved
include the thalamus, dorsolateral prefrontal cortex, ante-
iore explicitly with the modulation of one brain sy Intravenously as radiolabelled water infused over 2 min. left prefrontal cortex and the right lateral thalamic
Cotal counts per voxel during the build-up phase of radio-
ctivity served as an estimate of regional cerebral b along with their expression over the 12 scans. It is imme-The first- and second-order modes are seen in figure 4,
along with their expression over the 12 scans. It is imme-
diately apparent that the first mode reflects task-related
effects paralleling the alternation between word along with their expression over the 12 scans. It is immediately apparent that the first mode reflects task-related
effects paralleling the alternation between word genera-
tion and word shadowing. This profile of brain re effects paralleling the alternation between word generation and word shadowing. This profile of brain regions is effects paralleling the alternation between word generation and word shadowing. This profile of brain regions is
typical of verbal fluency paradigms that isolate the
intrinsic generation of semantic representations encodin tion and word shadowing. This profile of brain regions is
typical of verbal fluency paradigms that isolate the
intrinsic generation of semantic representations, encoding
and retrieval processes required to compare the curr typical of verbal fluency paradigms that isolate the
intrinsic generation of semantic representations, encoding
and retrieval processes required to compare the current
output with previous words and the maintenance of an intrinsic generation of semantic representations, encoding
and retrieval processes required to compare the current
output with previous words and the maintenance of an and retrieval processes required to compare the current
output with previous words and the maintenance of an
appropriate cognitive set. The key regions involved
include the thalamus dorsolateral prefrontal cortex anteoutput with previous words and the maintenance of an appropriate cognitive set. The key regions involved
include the thalamus, dorsolateral prefrontal cortex, ante-
rior cinculate temporal cortices and cerebellum. The appropriate cognitive set. The key regions involved
include the thalamus, dorsolateral prefrontal cortex, ante-
rior cingulate, temporal cortices and cerebellum. The
second mode represents the other experimental factor include the thalamus, dorsolateral prefrontal cortex, anterior cingulate, temporal cortices and cerebellum. The second mode represents the other experimental factor, namely time or order effects. A nonlinear effect is evid rior cingulate, temporal cortices and cerebellum. The second mode represents the other experimental factor, namely time or order effects. A nonlinear effect is evident with increases in activity in the cerebellar thalamic second mode represents the other experimental factor,
namely time or order effects. A nonlinear effect is evident
with increases in activity in the cerebellar, thalamic and
left basotemporal regions. More interesting is th namely time or order effects. A nonlinear effect is evident
with increases in activity in the cerebellar, thalamic and
left basotemporal regions. More interesting is the second-
order mode that by implication reflects an i with increases in activity in the cerebellar, thalamic and
left basotemporal regions. More interesting is the second-
order mode that, by implication, reflects an interaction
between task-related responses and time i.e. ti left basotemporal regions. More interesting is the second-
order mode that, by implication, reflects an interaction
between task-related responses and time, i.e. time-
dependent increases in physiological responses elicite order mode that, by implication, reflects an interaction
between task-related responses and time, i.e. time-
dependent increases in physiological responses elicited by cognitive operations that distinguish between the two dependent increases in physiological responses elicited by
cognitive operations that distinguish between the two
tasks employed. This physiological adaptation in most
propounced in Broca's Area (Brodmann Area 44 in the cognitive operations that distinguish between the two
tasks employed. This physiological adaptation in most
pronounced in Broca's Area (Brodmann Area 44 in the
left prefrontal cortex and the right lateral thalamic tasks employed. This physiological adaptation in most
pronounced in Broca's Area (Brodmann Area 44 in the
left prefrontal cortex and the right lateral thalamic
regions). Broca's Area is traditionally associated with pronounced in Broca's Area (Brodmann Area 44 in the
left prefrontal cortex and the right lateral thalamic
regions). Broca's Area is traditionally associated with
speech production and appears to undergo a profound left prefrontal cortex and the right lateral thalamic
regions). Broca's Area is traditionally associated with
speech production and appears to undergo a profound
change in its relative activation during word shadowing regions). Broca's Area is traditionally associated with
speech production and appears to undergo a profound
change in its relative activation during word shadowing
and generation after the first pair of scaps that presumspeech production and appears to undergo a profound
change in its relative activation during word shadowing
and generation after the first pair of scans that, presumchange in its relative activation during word shadowing
and generation after the first pair of scans that, presum-
ably, reflects an underlying change in cognitive archi-
tecture or set. ably, reflects an underlying change in cognitive archi-

(b) *A fMRI study of colour and motion processing*

(i) *Data acquisition, experimental design and preprocessing*

The experiment was performed on a 2 Tesla Magnetom (i) Data acquisition, experimental design and preprocessing
The experiment was performed on a 2 Tesla Magnetom
VISION (Siemens, Erlangen, Germany) whole body MRI
system, equipped, with a head volume coil. Continuous The experiment was performed on a 2 Tesla Magnetom
VISION (Siemens, Erlangen, Germany) whole body MRI
system equipped with a head volume coil. Contiguous
multislice T^* -weighted fMRI images (TE – 40 ms: VISION (Siemen
system equipped
multislice T_2^* -w
64 mm \times 64 mm \times multislice T_2^* -weighted fMRI images (TE = 40 ms; $64 \text{ mm} \times 64 \text{ mm} \times 48 \text{ mm}$ 3 mm $\times 3 \text{ mm} \times 3 \text{ mm}$ voxels)

igure 3. Variance partitioning following a nonlinear PCA of

a PET verbal fluency study. (*a*) Observed activity in a voxel
 λ , the left inferior frontal gyrus (filled bars) and that predicted igure 3. Variance partitioning following a nonlinear PCA of
ie PET verbal fluency study. (a) Observed activity in a voxel
i the left inferior frontal gyrus (filled bars) and that predicted
in the basis of two sources and re PET verbal fluency study. (*a*) Observed activity in a voxel
1 the left inferior frontal gyrus (filled bars) and that predicted
1 n the basis of two sources and their interaction (open bars)
1 stimated with poplinear P i the left inferior frontal gyrus (filled bars) and that predicted
n the basis of two sources and their interaction (open bars)
stimated with nonlinear PCA. Activity is in units

were obtained with echoplanar imaging using an axial
slice orientation. The effective renetition time was 4.8 s. A were obtained with echoplanar imaging using an axial
slice orientation. The effective repetition time was 4.8 s. A
young right-handed subject was scanned under four were obtained with echoplanar imaging using an axial
slice orientation. The effective repetition time was 4.8 s. A
young right-handed subject was scanned under four
different conditions in six scan enochs intercalated with slice orientation. The effective repetition time was 4.8 s. A
young right-handed subject was scanned under four
different conditions, in six scan epochs, intercalated with
a low level (visual fixation) baseline condition. young right-handed subject was scanned under four different conditions, in six scan epochs, intercalated with a low level (visual fixation) baseline condition. The four different conditions, in six scan epochs, intercalated with
a low level (visual fixation) baseline condition. The four
conditions were repeated eight times in a pseudorandom
order giving 384 scans in total or 32 stimulatio a low level (visual fixation) baseline condition. The four conditions were repeated eight times in a pseudorandom
order giving 384 scans in total or 32 stimulation-baseline
epoch pairs. During all stimulation conditions th conditions were repeated eight times in a pseudorandom
order giving 384 scans in total or 32 stimulation-baseline
epoch pairs. During all stimulation conditions the subject
looked at dots back-projected on a screen by an L order giving 384 scans in total or 32 stimulation–baseline
epoch pairs. During all stimulation conditions the subject
looked at dots back-projected on a screen by an LCD
video projector. The four experimental conditions epoch pairs. During all stimulation conditions the subject
looked at dots back-projected on a screen by an LCD
video projector. The four experimental conditions
comprised the presentation of (i) radially moving dots looked at dots back-projected on a screen by an LCD
video projector. The four experimental conditions
comprised the presentation of (i) radially moving dots,
and (ii) stationary dots using (i) luminance contrast and video projector. The four experimental conditions
comprised the presentation of (i) radially moving dots,
and (ii) stationary dots, using (i) luminance contrast and
(ii) chromatic contrast in a two-by-two factorial design. comprised the presentation of (i) radially moving dots,
and (ii) stationary dots, using (i) luminance contrast and
(ii) chromatic contrast in a two-by-two factorial design.
I uminance contrast was established using isochro and (ii) stationary dots, using (i) luminance contrast and
(ii) chromatic contrast in a two-by-two factorial design.
Luminance contrast was established using isochromatic
stimuli (red dots on a red background or green dots (ii) chromatic contrast in a two-by-two factorial design.
Luminance contrast was established using isochromatic
stimuli (red dots on a red background or green dots on a
green background). Hue contrast was obtained by using Luminance contrast was established using isochromatic
stimuli (red dots on a red background or green dots on a
green background). Hue contrast was obtained by using
red (or green) dots on a green (or red) background and stimuli (red dots on a red background or green dots on a
green background). Hue contrast was obtained by using
red (or green) dots on a green (or red) background and
establishing isoluminance with flicker photometry. In th green background). Hue contrast was obtained by using
red (or green) dots on a green (or red) background and
establishing isoluminance with flicker photometry. In the
two movement conditions the dots moved radially from red (or green) dots on a green (or red) background and establishing isoluminance with flicker photometry. In the two movement conditions the dots moved radially from the centre of the screen, at $8^{\circ} s^{-1}$, to the periphery where they vanished This creates the impression of two movement conditions the dots moved radially from
the centre of the screen, at $8^{\circ} s^{-1}$, to the periphery where
they vanished. This creates the impression of optical flow.
By using these stimuli we honed to excite a the centre of the screen, at $8^{\circ} s^{-1}$, to the periphery where
they vanished. This creates the impression of optical flow.
By using these stimuli we hoped to excite activity in
visual motion systems and those specialize they vanished. This creates the impression of optical flow.
By using these stimuli we hoped to excite activity in visual motion systems and those specialized for colour By using these stimuli we hoped to excite activity in visual motion systems and those specialized for colour processing. Any interaction between these systems would be expressed in terms of motion-sensitive reponses that visual motion systems and those specialized for colour
processing. Any interaction between these systems would
be expressed in terms of motion-sensitive responses that
depended on the bue or luminance contrast subtending processing. Any interaction between these systems would
be expressed in terms of motion-sensitive responses that
depended on the hue or luminance contrast subtending
that motion be expressed in terms of motion-sensitive responses that depended on the hue or luminance contrast subtending that motion. pended on the hue or luminance contrast subtending
at motion.
The time-series were realigned, corrected for movement-
ated effects and spatially normalized into the standard

that motion.
The time-series were realigned, corrected for movement-
related effects and spatially normalized into the standard
space of Talairach & Tournoux (1988) using the subject's The time-series were realigned, corrected for movement-
related effects and spatially normalized into the standard
space of Talairach & Tournoux (1988) using the subject's
co-registered structural T, scan and nonlinear def related effects and spatially normalized into the standard
space of Talairach & Tournoux (1988) using the subject's
co-registered structural T_1 scan and nonlinear deforma-
tions (Friston *et al.* 1996c). The data were space of Talairach & Tournoux (1988) using the subject's co-registered structural T_1 scan and nonlinear deformations (Friston *et al.* 1996*c*). The data were spatially smoothed with a 6 mm isotronic Gaussian kernel. A co-registered structural T_1 scan and nonlinear deformations (Friston *et al.* 1996*c*). The data were spatially smoothed with a 6 mm isotropic Gaussian kernel. As in the PET example voxels were selected that showed sig tions (Friston *et al.* 1996*c*). The data were spatially smoothed with a 6 mm isotropic Gaussian kernel. As in the PETexample, voxels were selected that showed significant condition-specific effects according to a conven smoothed with a 6 mm isotropic Gaussian kernel. As in
the PET example, voxels were selected that showed signifi-
cant condition-specific effects according to a conventional the PET example, voxels were selected that showed significant condition-specific effects according to a conventional
SPM analysis (Friston *et al.* 1995*b*; Worsley & Friston
1995) This analysis used a multiple linear regr cant condition-specific effects according to a conventional
SPM analysis (Friston *et al.* 1995*b*; Worsley & Friston
1995). This analysis used a multiple linear regression and
condition-specific box car regressors convolv SPM analysis (Friston *et al.* 1995*b*; Worsley & Friston 1995). This analysis used a multiple linear regression and condition-specific box car regressors convolved with a haemodynamic response function. In this instance, 1995). This analysis used a multiple linear regression and condition-specific box car regressors convolved with a haemodynamic response function. In this instance, the number of voxels was exceeding large and we used a condition-specific box car regressors convolved with a haemodynamic response function. In this instance, the number of voxels was exceeding large and we used a higher threshold than in the PET analysis ($p=0.001$) and haemodynamic response function. In this instance, the number of voxels was exceeding large and we used a higher threshold than in the PET analysis ($p=0.001$) and included only those voxels that were posterior to the posterior commissure higher threshold than ir
included only those ve
posterior commissure. (ii) *Nonlinear PCA*

The data were again reduced to an eight-dimensional (ii) *Nonlinear PCA*
The data were again reduced to an eight-dimensional
subspace using SVD and entered into the nonlinear PCA
using two sources. The functional attribution of these The data were again reduced to an eight-dimensional subspace using SVD and entered into the nonlinear PCA using two sources. The functional attribution of these sources was established by looking at the expression of the subspace using SVD and entered into the nonlinear PCA
using two sources. The functional attribution of these
sources was established by looking at the expression of the
corresponding first-order modes over the four conditi using two sources. The functional attribution of these
sources was established by looking at the expression of the
corresponding first-order modes over the four conditions. sources was established by looking at the expression of the corresponding first-order modes over the four conditions.
The expression of epoch-related responses over all 32 stimulation-baseline epoch pairs are shown in term corresponding first-order modes over the four conditions.
The expression of epoch-related responses over all 32
stimulation-baseline epoch pairs are shown in terms of
the four conditions in figure 5. This expression is sim The expression of epoch-related responses over all 32
stimulation-baseline epoch pairs are shown in terms of
the four conditions in figure 5. This expression is simply
the score on the first principal component over all 32 stimulation-baseline epoch pairs are shown in terms of
the four conditions in figure 5. This expression is simply
the score on the first principal component over all 32
epoch-related responses for each source. The first mo the score on the first principal component over all 32

Figure 3 (*Cont.*) corresponding to regional cerebral Figure 3 (*Cont.*) corresponding to regional cerebral
perfusion in ml dl⁻¹ min⁻¹. (*b*) Variance, over all voxels
included in the analysis, accounted for by the two sources Figure 3 (*Cont.*) corresponding to regional cerebral
perfusion in ml dl⁻¹ min⁻¹. (*b*) Variance, over all voxels
included in the analysis, accounted for by the two sources (or
modes) and their interaction Total – 88% perfusion in ml dl⁻¹ min⁻¹. (*b*) Variance, over all voxels
included in the analysis, accounted for by the two sources (or
modes) and their interaction. Total = 88%. (*c*) Distribution
of variance accounted for by sec included in the analysis, accounted for by the two sources (or modes) and their interaction. Total = 88% . (c) Distribution of variance accounted for by second-order or interaction modes) and their interaction. Total = 88% . (c) Distribution
of variance accounted for by second-order or interaction
effects over the conventional eigenimages obtained in the
initial SVD dimension reduction of variance accounted for by seconceffects over the conventional eigeni
initial SVD dimension reduction.

Figure 4. Maximum intensity projections and expression of the first- and second-order spatial modes of the PET verbal fluency
Figure 4. Maximum intensity projections and expression of the first- and second-order spatial mo study. (i) Spatial mode 1, (ii) spatial mode 2, and (iii) second-order mode. The maximum intensity projections *(a) are of the* maximum intensity projections *(a) are of the* maximum intensity projections *(a) are of the* positive values of each mode and septession of the first- and second-order spatial modes of the PET verbal fluency
pudy. (i) Spatial mode 1, (ii) spatial mode 2, and (iii) second-order mode. The maximum intensity projecti back and the top of the brain. The projections have been scaled to the maximum intensity projections (*a*) are of the ositive values of each mode and are displayed in standard format. The three orthogonal brain views are ositive values of each mode and are displayed in standard format. The three orthogonal brain views are from the right, the ack and the top of the brain. The projections have been scaled to the maximum intensity of each mo ack and the top of the brain. The projections have been scaled to the maximum intensity of each mode. The time-dependen
xpression of these modes are in terms of the 12 scans (b) . The units are adimensional and their abso the variance they account for is determined by the scaling of the spatial modes which, in turn, is dictated by the sigmoid quashing function, see figure 3).

 $\frac{c}{\alpha}$

learly a motion-sensitive mode but one that embodies learly a motion-sensitive mode but one that embodies
ome colour preference in the sense that the motion-
energient responses of this system are accentuated in the learly a motion-sensitive mode but one that embodies
one colour preference in the sense that the motion-
ependent responses of this system are accentuated in the
response of colour cues. This was not quite what we had presence of this system are accentuated in the resence of colour cues. This was not quite what we had nicinated: the first-order effect contains what would

ependent responses of this system are accentuated in the concerned exclusively with colour processing in the sense
resence of colour cues. This was not quite what we had that its expression is uniformly higher under colour functionally be called an interaction between motion and
colour processing. The second source appears to be functionally be called an interaction between motion and
colour processing. The second source appears to be
concerned exclusively with colour processing in the sense functionally be called an interaction between motion and
colour processing. The second source appears to be
concerned exclusively with colour processing in the sense
that its expression is uniformly bigher under colour colour processing. The second source appears to be concerned exclusively with colour processing in the sense that its expression is uniformly higher under colour stimuli relative to isochromatic stimuli in a way that does concerned exclusively with colour processing in the sense
that its expression is uniformly higher under colour
stimuli relative to isochromatic stimuli in a way that does

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condition
Figure 5. Condition-specific expression of the two first-order
andes ensuing from the visual processing fMRI study igure 5. Condition-specific expression of the two first-order ensuing from the visual processing fMRI study.
Sheed at a represent the degree to which the first principal igure 5. Condition-specific expression of the two first-order
rodes ensuing from the visual processing fMRI study.
hese data represent the degree to which the first principal
component of enoch-related waveforms over the rodes ensuing from the visual processing fMRI study.

"hese data represent the degree to which the first principal

"omponent of epoch-related waveforms over the 32 photic

"imulation baseline nairs was expressed These con These data represent the degree to which the first principal omponent of epoch-related waveforms over the 32 photic
imulation-baseline pairs was expressed. These condition-
exifectionomponent of epoch-related waveforms over the 32 photic
imulation–baseline pairs was expressed. These condition-
pecific responses are plotted in terms of the four conditions
we the two modes motion motion present; state st for the two modes. These condition-
pecific responses are plotted in terms of the four conditions
or the two modes. motion, motion present; stat., stationary
ots: colour isoluminant chromatic contrast stimuli: isoch pecific responses are plotted in terms of the four conditions
or the two modes. motion, motion present; stat., stationary
ots; colour, isoluminant, chromatic contrast stimuli; isoch.,
ochromatic luminance contrast stimuli or the two modes. motion, motion present; stat., stationary
ots; colour, isoluminant, chromatic contrast stimuli; isoch.
ochromatic, luminance contrast stimuli. (*a*) First-order
orde 1. (*h*) first-order mode 2. ots; colour, isoluminant, chrom
de 1, (*b*) first-order mode 2.

ot depend on motion. The corresponding anatomical profile is seen in figure 6 (maximum intensity projections)
profile is seen in figure 6 (maximum intensity projections)
is figure 6a and thresholded axial sections in figure 6b or depend on motion. The corresponding anatomical

profile is seen in figure 6 (maximum intensity projections)

i figure 6*a* and thresholded axial sections in figure 6*b*).

The first-order mode which shows both motion a The corrections of the seen in figure 6 (maximum intensity projections)
 $\frac{1}{2}$ figure $6a$ and thresholded axial sections in figure $6b$).

The first-order mode, which shows both motion and
 $\frac{1}{2}$ colour-related The first-order mode, which shows both motion and all oldur-related responses, shows high loadings in bilateral The first-order mode, which shows both motion and
olour-related responses, shows high loadings in bilateral
otion-sensitive complex V5 (Brodmann Areas 19 and 37
the occinto-temporal iunction) and areas traditionally olour-related responses, shows high loadings in bilateral
ation-sensitive complex V5 (Brodmann Areas 19 and 37
t the occipto-temporal junction) and areas traditionally
sociated with colour processing $(N4$ —the lingual notion-sensitive complex V5 (Brodmann Areas 19 and 37
t the occipto-temporal junction) and areas traditionally
sociated with colour processing (V4—the lingual
 Ω yrus Brodmann Area 19 ventromedially) The second t the occipto-temporal junction) and areas traditionally
ussociated with colour processing (V4—the lingual \overline{Q} yrus, Brodmann Area 19 ventromedially). The second sociated with colour processing $(V4$ —the lingual

syrus, Brodmann Area 19 ventromedially). The second

rst-order mode is most prominent in the hippocampus,

rabinnocampul and related lingual cortices on both) yrus, Brodmann Area 19 ventromedially). The second
rst-order mode is most prominent in the hippocampus,
arahippocampal and related lingual cortices on both
des The two more lateral blobs subsume the tails of the rst-order mode is most prominent in the hippocampus,
arahippocampal and related lingual cortices on both
des. The two more lateral blobs subsume the tails of the
audate nuclei (figure $6h(ii)$) This system is not one arahippocampal and related lingual cortices on both
des. The two more lateral blobs subsume the tails of the
audate nuclei (figure $6b(ii)$). This system is not one

be noted that some of the main effect of colour has been
explained by the first mode that includes V4. In
summary the two first-order modes comprise (i) an be noted that some of the main effect of colour has been
explained by the first-order that includes V4. In
summary, the two first-order modes comprise (i) an
extrastriste cortical system including V5 and V4 that summary, the two first-order modes comprise (i) an extrastriate cortical system including V5 and V4 that responds to motion, and preferentially so when motion is extrastriate cortical system including V5 and V4 that
responds to motion, and preferentially so when motion is
supported by colour cues; and (ii) a (para)hippocampal-
lingual system that is concerned exclusively with colou responds to motion, and preferentially so when motion is
supported by colour cues; and (ii) a (para)hippocampal-
lingual system that is concerned exclusively with colour
processing above and beyond that accounted for by th supported by colour cues; and (ii) a (para)hippocampal-
lingual system that is concerned exclusively with colour
processing, above and beyond that accounted for by the
first system. The critical question is where do these lingual system that is concerned exclusively with colour processing, above and beyond that accounted for by the first system. The critical question is where do these modes interact? processing,
first system.
interact?
The inte st system. The critical question is where do these modes
teract?
The interaction between the extrastriate and (para)
procampal-lingual systems conforms to the second-

interact?
The interaction between the extrastriate and (para)
hippocampal-lingual systems conforms to the second-The interaction between the extrastriate and (para)
hippocampal-lingual systems conforms to the second-
order mode in the lower panels. This mode highlights the
pulvinar of the thalamus and V5 bilaterally. This is a hippocampal–lingual systems conforms to the second-
order mode in the lower panels. This mode highlights the
pulvinar of the thalamus and V5 bilaterally. This is a
pleasing result in that it clearly implicates the thalamus order mode in the lower panels. This mode highlights the
pulvinar of the thalamus and V5 bilaterally. This is a
pleasing result in that it clearly implicates the thalamus in
the integration of extrastriate and (para)hippoc pulvinar of the thalamus and V5 bilaterally. This is a pleasing result in that it clearly implicates the thalamus in the integration of extrastriate and (para)hippocampal pleasing result in that it clearly implicates the thalamus in
the integration of extrastriate and (para)hippocampal
systems. This integration being mediated by recurrent
(sub)corticathalamic connections. It is also a resul the integration of extrastriate and (para)hippocampal
systems. This integration being mediated by recurrent
(sub)corticothalamic connections. It is also a result that
would not have obtained from a conventional SPM systems. This integration being mediated by recurrent
(sub)corticothalamic connections. It is also a result that
would not have obtained from a conventional SPM
analysis. Indeed we looked for an interaction between (sub)corticothalamic connections. It is also a result that would not have obtained from a conventional SPM analysis. Indeed we looked for an interaction between would not have obtained from a conventional SPM
analysis. Indeed we looked for an interaction between
motion and colour processing and did not see any such
effect in the pulvinar. The reason that the poplinear PCA analysis. Indeed we looked for an interaction between
motion and colour processing and did not see any such
effect in the pulvinar. The reason that the nonlinear PCA
was able to find this interaction was that there were no motion and colour processing and did not see any such
effect in the pulvinar. The reason that the nonlinear PCA
was able to find this interaction was that there were no
constraints on the sources underlying the interaction effect in the pulvinar. The reason that the nonlinear PCA was able to find this interaction was that there were no constraints on the sources underlying the interaction. In a was able to find this interaction was that there were no
constraints on the sources underlying the interaction. In a
conventional SPM analysis the sources are explicitly
assumed to be colour and motion in the visual field constraints on the sources underlying the interaction. In a
conventional SPM analysis the sources are explicitly
assumed to be colour and motion in the visual field,
whereas the two interacting modes identified by the assumed to be colour and motion in the visual field, whereas the two interacting modes identified by the assumed to be colour and motion in the visual field,
whereas the two interacting modes identified by the
nonlinear PCA were caused by complicated admixtures of
colour and motion. This result is presented to illustrate whereas the two interacting modes identified by the
nonlinear PCA were caused by complicated admixtures of
colour and motion. This result is presented to illustrate
the potential usefulness of poplinear PCA, not to make nonlinear PCA were caused by complicated admixtures of
colour and motion. This result is presented to illustrate
the potential usefulness of nonlinear PCA, not to make
any statistical inferences about reproducible function colour and motion. This result is presented to illustrate
the potential usefulness of nonlinear PCA, not to make
any statistical inferences about reproducible functional the potential usefulness of nonlinear PCA, not to make
any statistical inferences about reproducible functional
architectures. The exploratory analysis based on this case
study could now be used to motivate hypothesis-led any statistical inferences about reproducible functional
architectures. The exploratory analysis based on this case
study could now be used to motivate hypothesis-led
analyses of other subjects architectures. The explorate
study could now be used
analyses of other subjects. analyses of other subjects.
4. CONCLUSION

audate nuclei (figure $6b(ii)$). This system is not one nious characterization of functional neuroimaging time-
ormally associated with colour processing but it should series. 4. **CONCLUSION**
In this paper we have described a specific form of
plinear PCA that is predicated on the interaction 4. **CONCLUSION**
In this paper we have described a specific form of
nonlinear PCA that is predicated on the interaction
hetween underlying sources in modulating spatial modes In this paper we have described a specific form of
nonlinear PCA that is predicated on the interaction
between underlying sources in modulating spatial modes
of brain activity. Its theoretical motivation stems directly nonlinear PCA that is predicated on the interaction
between underlying sources in modulating spatial modes
of brain activity. Its theoretical motivation stems directly
from a second-order approximation to the Taylor expanbetween underlying sources in modulating spatial modes
of brain activity. Its theoretical motivation stems directly
from a second-order approximation to the Taylor expan-
sion of any nonlinear function of sources that can of brain activity. Its theoretical motivation stems directly
from a second-order approximation to the Taylor expan-
sion of any nonlinear function of sources that can cause
multivariate observations. A simple, three-layer from a second-order approximation to the Taylor expansion of any nonlinear function of sources that can cause multivariate observations. A simple, three-layer neuronal sion of any nonlinear function of sources that can cause
multivariate observations. A simple, three-layer neuronal
network architecture is sufficient to identify or estimate
the underlying causes and associated first- and multivariate observations. A simple, three-layer neuronal
network architecture is sufficient to identify or estimate
the underlying causes and associated first- and second-
order spatial modes. The first-order modes corres network architecture is sufficient to identify or estimate
the underlying causes and associated first- and second-
order spatial modes. The first-order modes correspond to
conventional eigenimages or principal components a the underlying causes and associated first- and second-
order spatial modes. The first-order modes correspond to
conventional eigenimages or principal components and
the second-order modes describe the patterns of brain conventional eigenimages or principal components and conventional eigenimages or principal components and
the second-order modes describe the patterns of brain
activity that result from interactions among these
sources. The ensuing decomposition into first- and the second-order modes describe the patterns of brain
activity that result from interactions among these
sources. The ensuing decomposition into first- and
second-order components represents an exploratory activity that result from interactions among these
sources. The ensuing decomposition into first- and
second-order components represents an exploratory
analysis of the data that eschews some of the shortcomsources. The ensuing decomposition into first- and
second-order components represents an exploratory
analysis of the data that eschews some of the shortcomsecond-order components represents an exploratory
analysis of the data that eschews some of the shortcom-
ings of conventional PCA. In particular, nonlinear PCA
allows for the context-sensitive expression of spatial analysis of the data that eschews some of the shortcomings of conventional PCA. In particular, nonlinear PCA allows for the context-sensitive expression of spatial modes through second-order modes that can be interings of conventional PCA. In particular, nonlinear PCA
allows for the context-sensitive expression of spatial
modes through second-order modes that can be inter-
preted as the anatomical substrate of integration or allows for the context-sensitive expression of spatial
modes through second-order modes that can be inter-
preted as the anatomical substrate of integration or
modulation. The highly constrained form of nonlinear modes through second-order modes that can be inter-
preted as the anatomical substrate of integration or
modulation. The highly constrained form of nonlinear
PCA presented above has an intuitive interpretation in preted as the anatomical substrate of integration or
modulation. The highly constrained form of nonlinear
PCA presented above has an intuitive interpretation in
terms of pairwise interactions among underlying sources modulation. The highly constrained form of nonlinear
PCA presented above has an intuitive interpretation in
terms of pairwise interactions among underlying sources
and by virtue of this represents a useful and parsimo-PCA presented above has an intuitive interpretation in
terms of pairwise interactions among underlying sources
and by virtue of this represents a useful and parsimo-
nious characterization of functional neuroimaging timeterms of pairwise interactions among underlying sources
and by virtue of this represents a useful and parsimoseries.

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In this paper, we have chosen to illustrate the technique
sing the interaction between modes associated with In this paper, we have chosen to illustrate the technique
sing the interaction between modes associated with
algebra and motion processing. Nonlinear PCA could of In this paper, we have chosen to illustrate the technique
sing the interaction between modes associated with
old of all and motion processing. Nonlinear PCA could of
ourse be used in any situation where one expects the sing the interaction between modes associated with

Dolour and motion processing. Nonlinear PCA could of

ourse be used in any situation where one expects the

civity of a distributed brain system to be modulated by by older and motion processing. Nonlinear PCA could of ourse be used in any situation where one expects the civity of a distributed brain system to be modulated by be expression of another system. Many examples come to ourse be used in any situation where one expects the ctivity of a distributed brain system to be modulated by he expression of another system. Many examples come to ind that may, or may not, be grounded in cognitive ctivity of a distributed brain system to be modulated by zience or neuroscience models. For example: Are the

modes implicated in the visual processing of word forms
and graphemes modulated by semantic modes in more modes implicated in the visual processing of word forms
and graphemes modulated by semantic modes in more
anterior, temporal, and, parietal, cortices? Although modes implicated in the visual processing of word forms
and graphemes modulated by semantic modes in more
anterior temporal and parietal cortices? Although
nonlinear PCA is an exploratory device and is implicitly and graphemes modulated by semantic modes in more
anterior temporal and parietal cortices? Although
nonlinear PCA is an exploratory device, and is implicitly
data-led careful experimental design can be used to anterior temporal and parietal cortices? Although
nonlinear PCA is an exploratory device, and is implicitly
data-led, careful experimental design can be used to
control the expression of various spatial modes that one nonlinear PCA is an exploratory device, and is implicitly
data-led, careful experimental design can be used to
control the expression of various spatial modes that one wishes to characterize. As a general point it is likely that the more powerful designs will be factorial in nature,

Characterizinginteractionsbetweenmodes of brain activity K. Friston and others 145 Downloaded from rstb.royalsocietypublishing.org

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an
allowing the expression of one mode, associated with one
verifierated factor to be assessed under different levels llowing the expression of one mode, associated with one sperimental factor, to be assessed under different levels f the expression of a second mode elicited by a second llowing the expression of one mode, associated with one
xperimental factor, to be assessed under different levels
f the expression of a second mode elicited by a second
xperimental cognitive or sepsory factor. In some xperimental factor, to be assessed under different levels
f the expression of a second mode elicited by a second
xperimental cognitive or sensory factor. In some
stances factorial designs are not always easy to f the expression of a second mode elicited by a second
xperimental cognitive or sensory factor. In some
istances, factorial designs are not always easy to
melement (e.g. in selective attention because it is difficult xperimental cognitive or sensory factor. In some istances, factorial designs are not always easy to nplement (e.g. in selective attention because it is difficult a attend selectively to a particular attribute when it is istances, factorial designs are not always easy to

uplement (e.g. in selective attention because it is difficult
 \rightarrow attend selectively to a particular attribute when it is
 \rightarrow ot present in the visual field). Howeve nplement (e.g. in selective attention because it is difficult
 σ attend selectively to a particular attribute when it is
 σ ot present in the visual field). However, many multi-

actorial experiments designed to loo factorial selectively to a particular attribute when it is
ot present in the visual field). However, many multi-
actorial experiments, designed to look at language
rocessing and memory, may lend themselves nicely to of present in the visual field). However, many multi-
actorial experiments, designed to look at language
rocessing and memory, may lend themselves nicely to
haracterization using the techniques described in this corrial experiments, designed to look at language
rocessing and memory, may lend themselves nicely to
haracterization using the techniques described in this
aper aper.

(a) *Extensions and limitations*

 \Box The limitations of the nonlinear PCA proposed above \Box re embodied in the constraints on the form of the (a) **Extensions and limitations**
The limitations of the nonlinear PCA proposed above
the embodied in the constraints on the form of the
examples on the form of the emposition assumed. The most obvious constraint is The limitations of the nonlinear PCA proposed above
re embodied in the constraints on the form of the
ecomposition assumed. The most obvious constraint is
lead it only allows for second-order interactions among The embodied in the constraints on the form of the
ecomposition assumed. The most obvious constraint is
allows for second-order interactions among
abunces or causes of the data, whereas higher-order interexemposition assumed. The most obvious constraint is
at it only allows for second-order interactions among
burces or causes of the data, whereas higher-order inter-
crions may prevail. It would of course, be easy to The state of the data, whereas higher-order interactions among
Dources or causes of the data, whereas higher-order inter-
ctions may prevail. It would, of course, be easy to
stend the neural net architecture to include thi External net architecture to include third-
crisis may prevail. It would, of course, be easy to
xtend the neural net architecture to include third- or
inher-order nodes and this may be justified in some data ctions may prevail. It would, of course, be easy to xtend the neural net architecture to include third- or igher-order nodes and this may be justified in some data analytic situations. In neuroimaging, however, the timeigher-order nodes and this may be justified in some data
nalytic situations. In neuroimaging, however, the time-
pries one deals with are usually quite short and noisy and
maly identifying second-order effects can be quite nalytic situations. In neuroimaging, however, the time-
second-order second-order effects can be quite ambi-
mply identifying second-order effects can be quite ambi-
ous The second limitation is that the number of sources Figure 5 one deals with are usually quite short and noisy and
mply identifying second-order effects can be quite ambi-
ous. The second limitation is that the number of sources
as to be prespecified. Again this may be a dra mply identifying second-order effects can be quite ambi-
ous. The second limitation is that the number of sources
as to be prespecified. Again this may be a drawback in ous. The second limitation is that the number of sources
as to be prespecified. Again this may be a drawback in
erms of system identification and independent compo-
ent analysis in general. However, in neuroimaging one as to be prespecified. Again this may be a drawback in
erms of system identification and independent compo-
ent analysis in general. However, in neuroimaging one
as experimental control over the number of factors (i.e. erms of system identification and independent compo-
ent analysis in general. However, in neuroimaging one
as experimental control over the number of factors (i.e.
surces) that are likely to cause neurophysiological ent analysis in general. However, in neuroimaging one
as experimental control over the number of factors (i.e.
burces) that are likely to cause neurophysiological as experimental control over the number of factors (i.e.
burces) that are likely to cause neurophysiological
hanges and specifying the number of sources is a much
pore tenable in terms of institutions contractions. burces) that are likely to cause neurophysiological
hanges and specifying the number of sources is a much
nore tenable, in terms of justifiable restrictions on the
asual model assumed for the data hanges and specifying the number
iore tenable, in terms of justifiable
asual model assumed for the data.
Another important consideration havior tenable, in terms of justifiable restrictions on the asual model assumed for the data.
Another important consideration is that, in the special

asual model assumed for the data.
Another important consideration is that, in the special
pplication of nonlinear PCA to functional imaging
ata an initial dimension reduction using SVD is Another important consideration is that, in the special
pplication of nonlinear PCA to functional imaging
ata, an initial dimension reduction using SVD is
equired This is because there are many more voxels pplication of nonlinear PCA to functional imaging
ata, an initial dimension reduction using SVD is
equired. This is because there are many more voxels
an observations It is well known that systematic errors ata, an initial dimension reduction using SVD is equired. This is because there are many more voxels nan observations. It is well known that systematic errors equired. This is because there are many more voxels
an observations. It is well known that systematic errors
an creep into applying SVD to simple nonlinear depen-
encies and that these depend on the rate of convergence an observations. It is well known that systematic errors
an creep into applying SVD to simple nonlinear depen-
encies and that these depend on the rate of convergence
of the Taylor series associated with equation (1) . I an creep into applying SVD to simple nonlinear depen-
encies and that these depend on the rate of convergence
of the Taylor series associated with equation (1). In this
aper the SVD is done first and then the nonlinear parameters and that these depend on the rate of convergence
 \int f the Taylor series associated with equation (1). In this

aper, the SVD is done first and then the nonlinear

nalysis is performed. It is always possible f the Taylor series associated with equation (1). In this to aper, the SVD is done first and then the nonlinear purishes is performed. It is always possible that the SVD as not established the right bases for the subsequen aper, the SVD is done first and then the nonlinear
nalysis is performed. It is always possible that the SVD
as not established the right bases for the subsequent analysis and that some bias will ensue. The result will be at apparent modulations of the first-order modes will nalysis and that some bias will ensue. The result will be
at apparent modulations of the first-order modes will
of the correct. These issues represent areas of future
ork, and could be addressed using 'toy' nonlinear at apparent modulations of the first-order modes will
not be correct. These issues represent areas of future
look and could be addressed using `toy' nonlinear
look and sunthetic imaging data and by examining ot be correct. These issues represent areas of future
vork and could be addressed using 'toy' nonlinear
vstems and synthetic imaging data and by examining
vse sensitivity of the second-order modes to the degree of Fork and could be addressed using 'toy' nonlinear
Uystems and synthetic imaging data and by examining
De sensitivity of the second-order modes to the degree of
UD dimension reduction. Gystems and synthetic imaging data and by examining
C is sensitivity of the second-order modes to the degree of
VD dimension reduction.
A more biological consideration relates to the he sensitivity of the second-order modes to the degree of

mechanism of the interaction. In the examples presented A more biological consideration relates to the echanism of the interaction. In the examples presented bove, we have assumed that the interaction is expressed the neuronal level in terms of modulation of neuronal rechanism of the interaction. In the examples presented
bove, we have assumed that the interaction is expressed
t a neuronal level, in terms of modulation of neuronal
sponses and dynamics themselves. It should be borne in bove, we have assumed that the interaction is expressed
t a neuronal level, in terms of modulation of neuronal
esponses and dynamics themselves. It should be borne in
laid that interactions can also be expressed at the lev t a neuronal level, in terms of modulation of neuronal
exponses and dynamics themselves. It should be borne in
 Ω ind that interactions can also be expressed at the level
f the haemodynamic response to [pop-interaction] exponses and dynamics themselves. It should be borne in

ind that interactions can also be expressed at the level

in the haemodynamic response to [non-interacting]

euronal responses (e.g. Friston et al. 1998). This shou ind that interactions can also be expressed at the level
f the haemodynamic response to [non-interacting]
euronal responses (e.g. Friston *et al.* 1998). This should
e considered where there is a high degree of anatomical f the haemodynamic response to [non-interacting]
euronal responses (e.g. Friston *et al.* 1998). This should
e considered where there is a high degree of anatomical euronal responses (e.g. Friston *et al.* 1998). This should
e considered where there is a high degree of anatomical
onvergence between first-order modes that evidence a
rong interaction e considered where
onvergence betwee
rong interaction. *Phil. Trans. R. Soc. Lond.* B (2000)

By virtue of the iterative scheme used for learning in By virtue of the iterative scheme used for learning in
the neural net there is always the problem of local
minima and the associated dependency on starting esti-By virtue of the iterative scheme used for learning in
the neural net there is always the problem of local
minima and the associated dependency on starting esti-
mates. In our applications we start with the conventional the neural net there is always the problem of local
minima and the associated dependency on starting esti-
mates. In our applications, we start with the conventional
PCA solution and therefore ensure that the ensuing minima and the associated dependency on starting estimates. In our applications, we start with the conventional PCA solution and therefore ensure that the ensuing mates. In our applications, we start with the conventional
PCA solution and therefore ensure that the ensuing
modes and interactions always account for more variance
than the corresponding linear PCA. In this sense there i PCA solution and therefore ensure that the ensuing
modes and interactions always account for more variance
than the corresponding linear PCA. In this sense there is
a unique solution (for any given gradient descent scheme) modes and interactions always account for more variance
than the corresponding linear PCA. In this sense there is
a unique solution (for any given gradient descent scheme)
and this is the nearest to the solution where the than the corresponding linear PCA. In this sense there is
a unique solution (for any given gradient descent scheme)
and this is the nearest to the solution where the second-
order effects are zero. a unique solution (for a
and this is the nearest
order effects are zero.
Perhans the most into d this is the nearest to the solution where the second-
der effects are zero.
Perhaps the most interesting limitation of the technique
esented in this paper is buried in the assumption that

presented in this paper is buried in the technique
presented in this paper is buried in the assumption that
there exists a linear combination of the inputs that gives Perhaps the most interesting limitation of the technique
presented in this paper is buried in the assumption that
there exists a linear combination of the inputs that gives
the expression of the sources. This depends on th presented in this paper is buried in the assumption that
there exists a linear combination of the inputs that gives
the expression of the sources. This depends on the
assumption (see δ 2) that first- and second-order mo there exists a linear combination of the inputs that gives
the expression of the sources. This depends on the
assumption (see $\S 2$) that first- and second-order modes
are not collinear. As long as they are not collinear the expression of the sources. This depends on the assumption (see $\S 2$) that first- and second-order modes are not collinear. As long as they are not collinear there is always a set of feed-forward connection strengths assumption (see $\S 2$) that first- and second-order modes
are not collinear. As long as they are not collinear there is
always a set of feed-forward connection strengths that are not collinear. As long as they are not collinear there is
always a set of feed-forward connection strengths that
span the subspace of one first-order mode that is ortho-
gonal to all other modes (first and second order always a set of feed-forward connection strengths that
span the subspace of one first-order mode that is ortho-
gonal to all other modes (first and second order). What
are the implications of collinearity between a first span the subspace of one first-order mode that is orthogonal to all other modes (first and second order). What
are the implications of collinearity between a first- and
second-order mode? Collinearity means that the expres gonal to all other modes (first and second order). What
are the implications of collinearity between a first- and
second-order mode? Collinearity means that the expres-
sion of a first-order mode is itself sensitive to the are the implications of collinearity between a first- and
second-order mode? Collinearity means that the expres-
sion of a first-order mode is itself sensitive to the expres-
sion of another mode (i.e. the first- and secon second-order mode? Collinearity means that the expression of a first-order mode is itself sensitive to the expression of another mode (i.e. the first- and second-order sion of a first-order mode is itself sensitive to the expression of another mode (i.e. the first- and second-order modes are the same thing). The possibility of this speaks to two fundamentally different context-sensitive sion of another mode (i.e. the first- and second-order
modes are the same thing). The possibility of this speaks
to two fundamentally different context-sensitive effects.
The first is when the interaction between two modes modes are the same thing). The possibility of this speaks
to two fundamentally different context-sensitive effects.
The first is when the interaction between two modes or
causes is expressed as a second-order mode with a d to two fundamentally different context-sensitive effects.
The first is when the interaction between two modes or
causes is expressed as a second-order mode with a distri-
bution that is distinct from both first-order modes The first is when the interaction between two modes or
causes is expressed as a second-order mode with a distri-
bution that is distinct from both first-order modes. This is
the situation considered in this paper, and can causes is expressed as a second-order mode with a distribution that is distinct from both first-order modes. This is
the situation considered in this paper and can be
addressed using poplinear PCA as described above bution that is distinct from both first-order modes. This is
the situation considered in this paper and can be
addressed using nonlinear PCA as described above.
Second, the interaction may be expressed solely in terms the situation considered in this paper and can be addressed using nonlinear PCA as described above.
Second, the interaction may be expressed solely in terms
of the expression of one of the two first-order modes.
Here there is no second-order mode only a contextual Second, the interaction may be expressed solely in terms
of the expression of one of the two first-order modes.
Here there is no second-order mode only a contextual
expression of first-order modes. This second form of of the expression of one of the two first-order modes.
Here there is no second-order mode only a contextual
expression of first-order modes. This second form of
context-sepsitivity requires a different sort of approach Here there is no second-order mode only a contextual expression of first-order modes. This second form of context-sensitivity requires a different sort of approach expression of first-order modes. This second form of
context-sensitivity requires a different sort of approach
(nonlinear ICA) and is interesting because it may repre-
sents a true contextual effect with which the brain ha context-sensitivity requires a different sort of approach
(nonlinear ICA) and is interesting because it may repre-
sents a true contextual effect with which the brain has to
contend in everyday sensory processing (nonlinear ICA) and is interesting becausents a true contextual effect with which
contend in everyday sensory processing.

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to thank Gary Green
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