



Research

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Modelling verbal aggression, physical aggression and inappropriate sexual behaviour after acquired brain injury

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Understanding the underpinnings of behavioural disturbances following brain injury is of considerable importance, but little at present is known about the relationships between different types of behavioural disturbances. Here, we take a novel approach to this issue by using confirmatory factor analysis to elucidate the architecture of verbal aggression, physical aggression and inappropriate sexual behaviour using systematic records made across an eight-week observation period for a large sample ($n = 301$) of individuals with a range of brain injuries. This approach offers a powerful test of the architecture of these behavioural disturbances by testing the fit between observed behaviours and different theoretical models. We chose models that reflected alternative theoretical perspectives based on generalized disinhibition (Model 1), a difference between aggression and inappropriate sexual behaviour (Model 2), or on the idea that verbal aggression, physical aggression and inappropriate sexual behaviour reflect broadly distinct but correlated clinical phenomena (Model 3). Model 3 provided the best fit to the data indicating that these behaviours can be viewed as distinct, but with substantial overlap. These data are important both for developing models concerning the architecture of behaviour as well as for clinical management in individuals with brain injury.

1. Introduction

Acts of aggression are of clear social concern, with significant costs existing at both the economic (e.g. legal and prison costs) and the personal (e.g. psychological scarring) level. Accordingly, understanding the underpinnings of aggression is of considerable importance, yet little is known about the relationship between different forms of aggressive and inappropriate behaviours, especially in neuropsychological contexts. Here, we take a novel approach to this issue by exploring the architecture of behavioural disturbances in a sample of individuals with brain injury through confirmatory factor analysis. This approach provides a powerful window into the origins of aggression for a number of reasons. First, acts of aggression in this population are often significant in magnitude and frequency, moving our analyses beyond the more commonly reported student or normal population studies of aggression. Second, we were able to use a systematic and detailed database of aggressive behaviours recorded as they occurred over an eight-week observation period. Third, we investigated instances of inappropriate sexual behaviours alongside verbal and physical aggression in order to assess their links.

Disorders of behavioural regulation, including verbal aggression, physical aggression and inappropriate sexual behaviour, are problematic and relatively common sequelae of severe acquired brain injury [1–7]. While there have been a number of studies investigating the nature and clinical correlates of aggressive behaviours following brain injury [3,8–13], only a handful have looked

at inappropriate sexual behaviours [7,9,14–18]. Fewer still have addressed both aggressive and inappropriate sexual behaviours within the same sample of patients, with mixed results to date concerning the co-occurrence of these behaviours [7,17,18]. Moreover, our previously reported sample of 152 patients with brain injury [19] documented the only known multivariate analysis of co-occurrence between aggression and inappropriate sexual behaviour. In this study, we found statistical distinctions between verbal aggression, physical aggression and inappropriate sexual behaviour based on principal component analysis.

The limited work to date addressing the architecture of behavioural disturbances following brain injury, alongside the broader benefits that insights into the aetiology of aggression and inappropriate sexual behaviour can bring to theory development, motivated this study. To this end, we sought to examine an independent and larger sample of individuals with brain injury in order to provide a more powerful test of the behavioural structure through confirmatory factor analysis. This approach offers a rigorous and hypothesis-driven examination of the relative merits of a given model of observed behaviour compared with its competitor models, as well as an absolute test of how well the model can explain observed data [20].

The three models we tested were chosen to closely reflect key theoretical perspectives in the field. First, we fitted a model based on the widely used neuropsychological concepts of disinhibition [14] or dysexecutive syndrome [15]. According to this perspective, the reason why most of us do not usually show aggressive or inappropriate sexual behaviours in our daily lives is that we are able to exercise a substantial degree of inhibitory control. Brain injury (and especially frontal lobe damage) reduces the degree of inhibitory control, or makes inhibition more effortful. Based on this line of reasoning, instances of verbal aggression, physical aggression and sexually inappropriate behaviour should covary, as they all reflect a common loss of inhibitory control. Such a model, in its simplest form, would be represented by a single common latent factor loading on each of the indicators of aggression or sexual inappropriateness (figure 1*a*).

Our second model (figure 1*b*) was based on the common sense distinction (evident in the words themselves) of a difference between aggression and inappropriate sexual behaviour. From this perspective, verbal and physical aggression should covary (both are instances of ‘aggression’, even if one considers that physical aggression is the more severe) but they will be broadly unrelated to inappropriate sexual behaviours (except perhaps where these also involve aggression). While we therefore separated these factors in our second model, we also allowed them to correlate to some degree, in line with work suggesting that they are likely to be at least modestly correlated [19].

Our third theoretical model (figure 1*c*) was derived from these earlier results [19] with principal component analysis of data from a smaller and independent sample of 152 participants, in which we noted distinctions between verbal aggression, physical aggression and inappropriate sexual behaviour following acquired brain injury that were interpreted to reflect broadly distinct but correlated clinical phenomena.

(a) This study

To test these competing models, we compiled a large database of systematically recorded instances of verbal aggression,

physical aggression and inappropriate sexual behaviour exhibited by 301 participants with severe acquired brain injury. The participants had been admitted consecutively to seven specialist neurobehavioural rehabilitation centres across the UK and completed an eight-week assessment period. All incidents of these behaviours witnessed by staff over this period were recorded as they occurred by trained rehabilitation staff via specifically designed psychometric observational scales. These behavioural data, as well as relevant clinical data on the participants and their brain injuries, were extracted from individual participant clinical files. Owing to the comprehensive nature of the clinical programmes and the use of behavioural data in both individual assessment and organizational outcomes, there were no missing data for these participants. This approach is a substantial advance over many other studies investigating such behavioural disorders after brain injury, which are typically forced to rely on judgements by health professionals [11,16] and/or patients’ families [3,10,13] that are often made some time after the incidents in question. This introduces potential unwanted error arising from memory biases and distortions and therefore represents a major limitation to such studies. Frequency of occurrence and co-occurrence of different behaviours may be underestimated, overestimated or missed altogether without a contemporaneous method of recording [17]. Systematic contemporaneous recordings of the type we were able to use therefore constitute a gold standard for this type of study.

The participants we studied had a number of different types of precipitating brain injuries, and had been referred for residential assessment for a variety of reasons that all centred on the likelihood of significant neuropsychological sequelae. They can therefore be considered to represent the full range of types of impairment that might affect behavioural regulation. Using the systematic records of observed behaviour, we sought to test which of these three major competing theoretical models detailed above best fitted the patterns of disordered behaviour that were observed. In line with previous work indicating that aggression contains both distinct and overlapping components, we predicted that a model characterized by such features (i.e. Model 3) would provide the best fit to the data.

2. Material and method

(a) Participants

Three hundred and one participants were included from a total pool of admissions to seven organizational residential rehabilitation programmes across the UK during the period January 2010 to June 2012. Two of the programmes specialized in challenging behaviour, while the remaining five were classed as community re-integration (although one programme within a local hospital ward was also considered sub-acute rather than post-acute). Participants were included if they had completed at least nine weeks of residential neurobehavioural assessment, which included continuous behavioural observation and recording.

Two hundred and thirty-five (78%) of the participants were male and 66 female. Age at admission, which was normally distributed, ranged from 16 to 76 years, with a mean of 42.7 years and standard deviation of 14.6 years. Years of formal education ranged from 6 to 18, which was positively skewed and leptokurtic, with a median value of 10 years. The majority of the sample (93%) was identified as predominantly right-handed prior to their injury/illness.

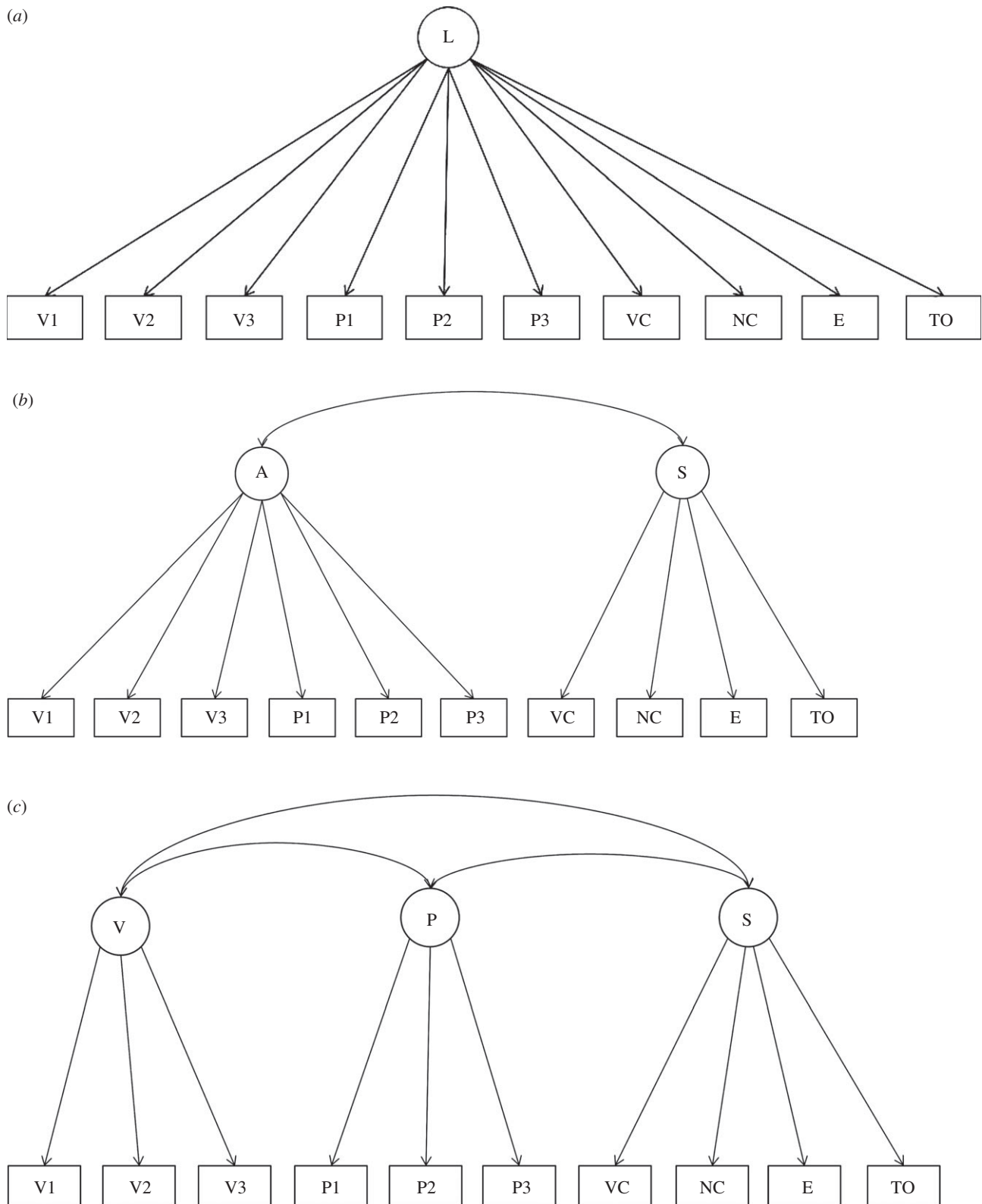


Figure 1. Graphical representation of Models 1, 2 and 3. (a) Model 1: single common factor model in which indices of verbal aggression (V1, V2 and V3) physical aggression (P1, P2 and P3) and inappropriate sexual behaviours (VC, NC, E and TO) are all related to a common latent variable (L), as might be expected from concepts such as disinhibition or dysexecutive syndrome. (b) Model 2: two distinct but correlated factors model based on an aggression (A) factor (verbal aggression V1, V2 and V3; physical aggression P1, P2 and P3) and a second inappropriate sexual behaviour (S) factor (VC, NC, E and TO). (c) Model 3: three distinct but correlated factors model based on a verbal aggression (V) factor (V1, V2 and V3), a physical aggression (P) factor (P1, P2 and P3) and an inappropriate sexual behaviour (S) factor (VC, NC, E and TO).

Data regarding severity of injury were incomplete but indicative of predominantly severe injuries. This is consistent with previous clinical research [18,21] in similar post-acute brain injury rehabilitation programmes and with our previously reported sample [19]. The most common diagnosis was traumatic

brain injury (56%), followed by cerebro-vascular accidents (22%) and cerebral anoxia (11%). Other types of injuries or illnesses made up 11% of the sample and included infectious diseases ($n = 16$), cerebral tumour ($n = 6$) and alcohol-related brain damage ($n = 4$).

Table 1. Raw frequency counts of aggression from the BARS (verbal aggression V1, V2 and V3; physical aggression P1, P2 and P3) and inappropriate sexual behaviours from the SASBA (VC, NC, E and TO). (The last four columns present the category percentages of the recorded data (for more detail, see the Material and methods section). For all variables: median = mode = 0 and $n = 301$.)

measure	range	mean	0	1	2	3
V1 (non-directed verbal aggression)	0–1042	8.91	56.15	8.31	11.30	24.25
V2 (directed verbal aggression)	0–348	7.73	54.49	7.97	13.95	23.59
V3 (verbal threats)	0–1036	9.95	68.77	5.65	7.31	18.27
P1 (non-directed physical aggression)	0–268	3.59	72.76	7.31	7.64	12.29
P2 (physical aggression towards property)	0–147	0.92	89.37	4.32	2.99	3.32
P3 (physical aggression towards people)	0–1219	12.26	72.09	5.32	7.97	14.62
VC (inappropriate sexual VC)	0–780	6.67	73.75	4.98	9.30	11.96
NC (inappropriate sexual NC behaviours)	0–227	1.81	87.04	3.65	4.98	4.32
E (inappropriate sexual E)	0–118	0.62	94.35	2.33	2.66	0.66
TO (inappropriate sexual TO)	0–467	3.06	83.72	2.99	6.98	6.31

The age at which the participants acquired their brain injuries or illnesses ranged from 1 to 75 years and was normally distributed, with mean age of 39.7 years and standard deviation 16.8 years. The time between injury/illness and admission to the rehabilitation programme ranged from one month to 636 months. These post-injury admission intervals were not normally distributed, being positively skewed and leptokurtic with a median chronicity of 5.9 months.

(b) Measures

Data were recorded across a continuous nine-week observation period used as part of the assessment of each patient in the hospital rehabilitation setting. To allow participants time to establish some kind of routine, data from the first week of observation were not analysed, leaving records across an eight-week period for each of 301 participants. During this time, all witnessed instances of physical aggression, verbal aggression and inappropriate sexual inappropriate behaviours were recorded by trained staff immediately after they were observed.

Aggressive behaviour was coded according to the Brain Injury Rehabilitation Trust (BIRT) Aggression Rating Scale (BARS), which has demonstrated good inter-rater reliability [22]. The BARS codes aggression into six categories reflecting the nature (verbal or physical) and severity (1, 2 or 3) of each episode. Incidents of verbal aggression are scored as V1 for non-directed, V2 for directed at another person or V3 for verbal threats. Similarly, incidents of physical aggression are scored as P1 for non-directed, P2 for damage to property and P3 for violence towards another person or one's self.

Episodes of inappropriate sexual behaviour were recorded by staff with the St Andrews Sexual Behaviour Assessment—SASBA [23]. This scale consists of four categories of behaviour (verbal comments, VC; non-contact, NC; exposure, E; and touching others, TO) with four severity levels within each category. This produces a matrix of 16 specific behaviour codes for inappropriate sexual behaviour. Examples of behaviours categorized using this system include: comments made directly to another person about their genitals (VC3), beginning to masturbate in own bedroom without exposing genitals when staff are present (NC3), intentionally exposing genitals to another person (E3), touching another person's buttocks (TO3)

Participants' behaviours were observed for the eight weeks of assessment in order to obtain a baseline from which later clinical decisions could be taken. For episodes in which more than one

behaviour was observed, the protocol was that staff recorded each type of behaviour; an episode of challenging behaviour was defined as having ended when the participant had returned to their baseline behaviour for at least 2 min. For each participant, all recorded incidents across the eight-week assessment period were summed for each of these 22 raw behavioural count variables. Six of these were derived from the BARS (verbal aggression V1, V2 and V3; physical aggression P1, P2 and P3) and 16 from the SASBA (verbal comments VC1, VC2, VC3 and VC4; non-contact NC1, NC2, NC3 and NC4; exposure E1, E2, E3 and E4; touching others TO1, TO2, TO3 and TO4). However, as in our previous study [19], each behavioural variable had a highly non-normal distribution with an excess of zero counts ($n = 114/37.87\%$ of the respondents showed patterns with zero count on all 10 variables). This was particularly the case for most of the SASBA codes. In consequence, we summed the SASBA data into the four categorical codes of VC, NC, E and TO.

(c) Analysis

All confirmatory factor models were fitted in R v. 3.1.2 [24] using mirt 1.8 [25]. We used the Metropolis–Hastings Robbins–Monro hybrid algorithm for estimation [26]. The program fits a multi-dimensional item response model to the data, which estimates a set of latent variables that together optimally predict the responses to the individual items. In our case, such latent variables could for example be 'disinhibition' (only a single latent variable influencing the responses to all items, figure 1*a*) or three related components of disturbed behaviour (figure 1*c*). The program uses a logistic link function to model the probability to respond in a specific category (i.e. frequency band, see columns 3–7 of table 1) of an item (i.e. type of behavioural incidents) [25], thereby explicitly taking the categorical nature of the data into account. For the multi-dimensional item response model, three types of parameters have to be estimated: (i) the loadings connecting the latent factors and the items; (ii) the correlations between the latent factors (if any); (iii) the so-called thresholds, i.e. the transition points between the categories of the individual items (here three per item; table 1); and (iv) an error term per item. To assess model fit, we used the Bayesian information criterion (BIC: [27]), where lower values indicate more parsimonious fit in model comparisons, the RMS error of approximation (RMSEA: excellent fit less than 0.05) and the comparative fit index (CFI: excellent fit more than 0.95).

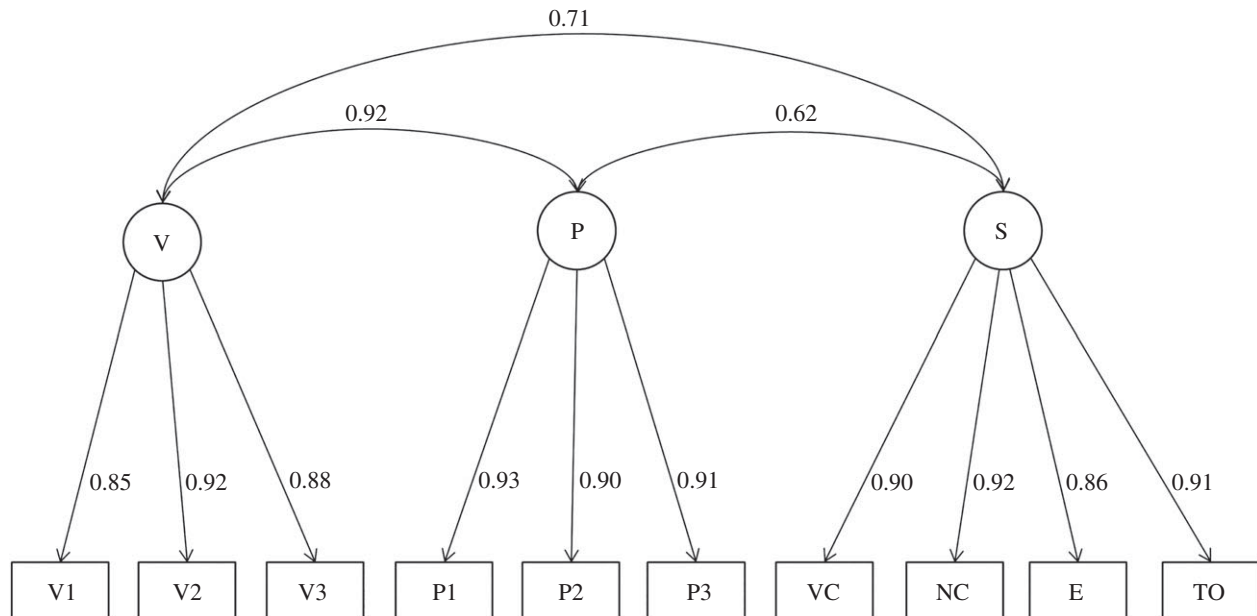


Figure 2. Final best fitting model (Model 3) based on an inter-correlated verbal aggression (V) factor (V1, V2 and V3), a physical aggression (P) factor (P1, P2 and P3) and an inappropriate sexual behaviour (S) factor (VC, NC, E and TO). All paths and inter-factor correlations are significant (less than 0.01).

Table 2. Fit statistics for theoretical models. (Italicized values denote best fitting model; CFI, comparative fit index; TLI, Tucker–Lewis index; $n(P)$, number of parameters; RMSEA, RMS error of approximation.)

model	log-likelihood	$n(P)$	BIC	RMSEA	TLI	CFI
1	-1873	40	3973	0.112	0.815	0.889
2	-1813	41	3861	0.045	0.970	0.983
3	<i>-1804</i>	<i>43</i>	<i>3853</i>	<i>0.00</i>	<i>1.0</i>	<i>1.0</i>

3. Results

The ranges of observed instances for each behavioural variable are presented in table 1. In brief, we observed substantial variability across each of the measures, but with many scores at zero or slightly above (median/mode = 0) for all variables.

(a) Model fitting

As detailed above, we tested a series of competing models (see figures 1 and 2). Model 1 was a common factor model with a single latent factor loading on all of the indicators. Model 2 contained two correlated common factors: the first for physical and verbal aggression and the second for inappropriate sexual behaviour items. Model 3, our hypothesized model, contained three correlated latent factors, with these factors loading on the verbal aggression, physical aggression and inappropriate sexual behaviour indicators, respectively.

Owing to the non-normality of the data, we adopted a categorical approach based on multi-dimensional item response theory [28] to fit our theoretical models. The data were extremely right-skewed and each item of the coding system had disproportionately many zero values. Although alternative possibilities were considered (see Discussion for further details), this categorical approach has at least two key advantages: (i) categorization makes it possible to deal with both zero-inflated and right-skewed data; and (ii) categorizing and then analysing the data with an item response model neither assumes that the categories are equidistant nor that the indicators are linearly

related, which allows for a better representation of data in the model. As such, the data were recoded into four categories: 0 instances of aggression/inappropriate sexual behaviour over the eight weeks = 0; 1 = 1; 2–4 = 2; 5 and above = 3. This coding scheme was deemed appropriate as it ensured for all recoded variables at least 10 responses per category (only for item 8 this was not possible).

Model output is detailed in table 2. Model 1 provided a poor fit to the data on all fit indices and so was rejected. Model 2 and Model 3 both provided a good fit to the data, although Model 3 showed a superior fit by all metrics. Owing to the sparse data in some of the cells in table 1, we also performed the analysis based on dichotomous data ('0' counts versus any observed behaviour) and again the structure was largely corroborated. This brought Models 2 and 3 even closer, both showing good fit RMSEA less than 0.05; CFI and Tucker–Lewis index more than 0.98; BIC difference less than 10 (about 4). In addition, results derived from alternative analytical approaches (i.e. data transformations or outlier removal: see Discussion for more details) again favoured Model 3 in every case, with Model 2 showing substantially lower fit across a range of indices. As such, we selected Model 3 as our final model (figure 2).

To facilitate clinical interpretation, we conducted a complementary analysis assessing the probability of displaying a given behaviour based on another one having been reported. These results are detailed in table 3. In short, these observations further illustrate differentiation in our sample between participants that show behavioural disturbance and those that do not.

Table 3. Probability of observing aggression or inappropriate sexual inappropriate behaviour in the absence/presence of other forms of aggression or inappropriate sexual behaviour. ($p(+|0)$ = the probability of at least one incident of aggressive or sexually inappropriate behaviour if no incidents are reported for the variable in question; $p(+|1)$ = the probability of at least one incident of aggressive or sexually inappropriate behaviour if one or more incidents are reported for the variable in question; $p(\text{VA} + |1)$ = the probability of at least one incident of verbal aggressive behaviour if one or more incidents are reported for the variable in question; $p(\text{PA} + |1)$ = the probability of at least one incident of physical aggressive behaviour if one or more incidents are reported for the variable in question; $p(\text{ISB} + |1)$ = the probability of at least one incident of sexually inappropriate behaviour if one or more incidents are reported for the variable in question.)

variable	$p(+ 0)$	$p(+ 1)$	$p(\text{VA} + 1)$	$p(\text{PA} + 1)$	$p(\text{ISB} + 1)$
V1 (non-directed verbal aggression)	0.09	0.40	—	0.23	0.16
V2 (directed verbal aggression)	0.07	0.41	—	0.21	0.22
V3 (verbal threats)	0.13	0.49	—	0.31	0.21
P1 (non-directed physical aggression)	0.14	0.53	0.74	—	0.19
P2 (physical aggression towards property)	0.22	0.63	0.77	—	0.27
P3 (physical aggression towards people)	0.14	0.51	0.67	—	0.25
VC (inappropriate sexual VC)	0.16	0.49	0.56	0.29	—
NC (inappropriate sexual NC behaviours)	0.21	0.62	0.70	0.42	—
E (inappropriate sexual E)	0.25	0.64	0.81	0.48	—
TO (inappropriate sexual TO)	0.19	0.60	0.78	0.52	—

As soon as any aggressive or sexually inappropriate behaviour is recorded for a given patient, there is a probability of between 0.40 and 0.64 that any other aggressive or sexually inappropriate behaviour will be observed as well. Columns four to six of table 3 provide information on the predictive power of the individual behaviours. Participants showing physical aggression and inappropriate sexual behaviour are very likely to also show verbal aggression (all $p(\text{verb} + |1) > 0.50$). The probabilities for the other two are markedly lower; inappropriate sexual behaviour is particularly difficult to predict from verbal and physical aggression.

4. Discussion

This study sought to test the factor structure of aggressive and inappropriate sexual behaviours in a clinical sample. A model based on considering physical aggressiveness, verbal aggressiveness and sexually inappropriate behaviours as reflecting distinct but correlated clinical phenomena (Model 3) offered the best comparative fit to the data. Moreover, this model also provided a good absolute fit to the data. It is noteworthy, however, that Model 2—positing two correlated latent factors reflecting aggression and sexually inappropriate behaviours—also provided a good fit to the data and was only marginally inferior to Model 3. This observation is discussed in more detail below.

These findings have important implications for the widely used concept of a general disinhibition (or executive deficits) of behavioural impulses. Model 1—designed to reflect a general loss of inhibitory control—was unable to provide a full explanation of the covariation across different forms of aggressive and inappropriate sexual behaviour. Although specific regions of the prefrontal cortex (and associated networks) have been proposed to underlie the process of inhibitory control in terms of acting as a cerebral ‘brake’ over behavioural impulses [29], the conceptual status of disinhibition has already been brought into question [30]. This study shows its empirical limitations.

As well as their implications for modelling and understanding what are usually considered challenging behaviours, the findings have two substantial clinical implications. First, these results provide support for assessing and formulating these behaviours separately within the context of behavioural management in individuals with acquired brain injury. This is consistent with previously reported analyses [7,31] showing differing maintaining factors and environmental triggers for aggression and inappropriate sexual behaviour after brain injury. A recent intervention case study [32] also documented the specificity of treatment effects for inappropriate sexual behaviour in a young man following severe traumatic brain injury.

Second, the results of our complementary analyses presented in table 3 provide information concerning the relative risk of individuals demonstrating other forms of behavioural disturbance when some disturbance has already been observed. This will be of considerable use to clinicians undertaking risk assessments for admission of individuals with challenging behaviour into residential facilities. For example, individuals demonstrating verbal aggression have a relatively low likelihood of also exhibiting physical aggression or inappropriate sexual behaviour. Conversely, individuals demonstrating physical aggression are likely to also exhibit verbal aggression but not inappropriate sexual behaviour. For those individuals displaying inappropriate sexual behaviour, there is also a relatively high risk of exhibiting verbal aggression. The risk of also exhibiting physical aggression is lower, although it becomes higher with the more severe forms of observed inappropriate sexual behaviour. Specifically, the risk of any physical aggression with the lowest level of inappropriate sexual behaviour (through verbal comments) is relatively low (0.29) but steadily increases with the severity of inappropriate sexual behaviour, so that physical aggression in the context of sexually inappropriately TO becomes more likely than not (0.52).

Some discussion is required with regards to our analytical approach in light of the highly non-normal distribution of the data. We opted to use a categorical analysis as our main approach, as well as reporting results from analyses using

dichotomized indicators; however, we also considered alternative approaches, including applying different transformations of the original count data (logarithm, square-root), or the exclusion of outliers (based on Mahalanobis distances; [33]). The purpose of these transformations was to try to accommodate the severe non-normality of the data, but it turned out that even transformations of this kind were insufficient to normalize the data. The consequence of this failure to achieve normality is that absolute fit indices—which are heavily dependent on normality and linearity of the observed variables—will be negatively impacted, even when an appropriate model is examined. As such this further confirms the value of the categorical approach adopted here, which is free of these assumptions [34].

Results from these analyses are still of some value, however, and support the conclusion that Model 3 was the appropriate choice as final model. While results differed in detail across these transformations of the data, overall Model 3 always fitted the data better than Model 2, with the latter showing a similar fit to the former only in our categorical and the dichotomized analyses. However, given that Model 2 fitted the data well in our core analyses, and the high correlation observed between the physical and verbal aggression factors in Model 3, alongside the possibility that the high values observed for the fit indices of Model 3 might be partly due to overfitting, future work is nonetheless recommended to further probe the fine-grained architecture of these behaviours in order to provide further insights on the degree of dissociability that exists between verbal and physical aggression.

Other limitations and recommendations for future research require discussion. First, one limitation of the dataset is the potential impact that staff intervention (such as the use of de-escalation strategies) may have had on incidents involving aggressive and inappropriate sexual behaviour. It is likely that clinical management of these situations would

serve in some instances to either increase or decrease the range and severity of further observed behaviours. Unfortunately, we did not have detailed information regarding this. As such, the impact of different interventions remains an area for further investigation.

Second, future studies could also address whether the structural architecture observed here is consistent across subsections of the population with severe brain injury. For example, some studies have reported that males are more likely to behave aggressively after brain injury [12,13], while others have not [19,35]; males have more consistently been identified as considerably more likely to demonstrate inappropriate sexual behaviour [16,36].

In summary, here we find evidence for dissociable yet correlated components of verbal aggression, physical aggression and inappropriate sexual behaviours using systematic records made across an eight-week observation period for a large clinical sample of adults with severe brain injuries. Complementary analyses demonstrated that, when a particular behaviour had been observed, the probability of another form of aggressive or inappropriate sexual behaviour occurring was high (between 0.40 and 0.64).

Ethics. Ethics approval for this study was granted by the University of York and The Disabilities Trust. As this was an archival study of routine clinical data, participants were not required to provide informed consent.

Data accessibility. Raw and categorized behavioural data can be found in the Dryad Digital Repository: <http://doi.org/10.5061/dryad.42vq4>.

Authors' contributions. A.J. and A.Y. conceived of the study; A.J. collected the behavioural data; J.B. and G.L. formulated the models and the analytic strategy; J.B. conducted the statistical analyses; A.Y. coordinated the study. All authors helped draft the manuscript and gave final approval for publication.

Competing interests. We declare we have no competing interests.

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