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Phil. Trans. R. Soc. B 2010 **365**, 4043-4050

doi: 10.1098/rstb.2010.0061

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Review

Personality: bridging the literatures from human psychology and behavioural ecology

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The concept of personality has recently begun to attract a great deal of interest in behavioural ecology. However, there is also a large and mature literature on personality within human psychology. These two bodies of work have developed independently and at present make rather little reference to one another. The current paper has two main objectives. First, we seek to acquaint behavioural ecologists with the principal ideas and issues found in the human personality psychology literature. Second, we explore how ideas from the behavioural ecology literature might help advance research in human personality psychology. We suggest strong potential for convergence between the two literatures in the near future. Common themes of this future unified science of personality include the conception of personality traits as reaction norms, a commitment to the importance of direct measurement of behaviour, investigation of both proximate and ultimate explanations for personality variation, and a concern with the impact of personality variation on survival and reproductive success.

Keywords: personality; behavioural reaction norms; behavioural ecology; five-factor model

1. INTRODUCTION

Animal personality has begun to receive a great deal of attention from behavioural ecologists, as the papers in this issue attest. Personality in the behavioural ecology (henceforth, BE) literature refers to consistent differences in behaviour among individuals from the same species or population, even if they experience the same ecological conditions. Such differences were frequently ignored, or treated as noise, in classic BE research, where the focus was often on comparing the central tendency of animals' behaviour to a normative model (as, for example, in optimal foraging theory). However, in recent years, researchers have increasingly recognized that individual differences in behaviour in a given environment are substantial, and that these differences pose interesting questions in their own right (Wilson 1998; Dingemanse & Réale 2005). For example, we can identify the proximate genetic or environmental causes of adult differences in phenotype. We can also ask how natural selection acts on the population distribution of phenotypes, often maintaining diversity through balancing selection pressures. Finally, we can ask why selection causes different phenotypic traits to come to covary, when other patterns of covariance would be equally possible.

The concept of personality is not an original innovation of BE, though. Within human psychology,

there has been a tradition of research in personality (henceforth HPP, human personality psychology) stretching back at least 100 years. Indeed, the study of personality has been one of psychology's central concerns. Despite this, the two literatures at present remain rather unintegrated (see van Oers 2007). Reviews of BE animal personality research make relatively little reference to the HPP literature, while the burgeoning BE evidence is scarcely discussed in the pages of HPP journals. Our aim in this paper is thus to introduce these two research areas, independently evolved but with much common potential interest, to one another. We will hope to show BE researchers that the methodological traditions and explanatory concerns of HPP have been somewhat different from those familiar to behavioural ecologists, but that the HPP literature nonetheless contains much of relevance for them. We will also argue that the BE literature provides inspiration for clarifying certain issues within HPP. We conclude, optimistically, that BE and HPP are converging towards a notion of personality as behavioural reaction norm, and that this allows the two fields to define and pursue a unified set of questions.

In what follows, we first provide a brief and partial overview of HPP research as it has developed (§2). We then lay out some of the controversies which have detained personality psychologists, and suggest how thinking in behavioural ecological terms can be of use in resolving these (§3). Finally, we conclude optimistically that there is potential for conceptual unification of the BE and HPP literatures in the future.

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One contribution of 16 to a Theme Issue 'Evolutionary and ecological approaches to the study of personality'.

2. A BRIEF OVERVIEW OF HUMAN PERSONALITY RESEARCH

The impulse behind research in HPP begins with the simple observation that the people we meet are different from one another in their behaviour. More than that, they are characteristically different. That is, if Bob is nervous in one year's exams, it seems likely that he will be nervous in the next year's exams too, and this tempts us to ascribe some stable internal feature to Bob ('exam nerves'), which is part of what we call his personality. Such observations are the foundation of HPP research, and seem straightforward enough. However, an outsider plunging into the HPP literature is confronted by apparent disunity. There are several different traditions of research, which often criticize and sometimes even ignore each other, and each forefronts different constructs. For example, some authors champion the five-factor approach (the idea that important human personality variation can be adequately characterized using five continuous and roughly orthogonal axes) as the overall foundation of the field (Costa & McCrae 1992; John Naumann & Soto 2008), while others use different numbers of dimensions (Eysenck 1992; Ashton *et al.* 2004), or are sceptical about all dimension-based frameworks, and propose quite different types of constructs and theories for thinking about personality variation (see Cervone 2004; Cervone & Shoda 1999, and the exchange between Sheldon *et al.* (2007) and Nettle (2007)).

Where such disagreement is found in science, it is often the case that different researchers simply have different objectives. We will thus organize our review of some of the major developments in HPP around the different objectives that different parts of the literature pursue. The five objectives we cover are basic descriptive work; study of proximate mechanisms; identification of genetic and environmental influences; fitness consequences of personality; and, finally, comparative personality research.

(a) *Descriptive work*

Perhaps the largest single body of research—what we will call the *trait identification tradition* (e.g. Cattell 1965; Goldberg 1990; McCrae & Costa 1985, 1987; Ashton *et al.* 2004)—has been concerned with the description of population variation. Unlike personality research in BE, which tends to focus on particular behavioural dimensions that are most salient in domains of interest (e.g. boldness during exploration or aggressiveness towards predators), HPP places much value on identifying *comprehensive* descriptions of personality structure. The most established attempts to comprehensively describe personality structure are based on the *lexicographic approach*. This assumes that every major behavioural dimension in humans should be reflected in the vocabulary people use to talk about other people or themselves. Words that can be used to describe people's behaviour and dispositions (like 'anxious' or 'shy') have been systematically extracted from the dictionaries of many languages and were then given to individuals to rate how well these words describe themselves or others.

Factor analysis can then be employed to extract the (much smaller) number of personality dimensions required to describe variation in ratings in the samples (John *et al.* 2008). Much effort is expended on exactly which factorial solutions are preferred, and what each of the dimensions should be called (e.g. Boyle 1989; Gerbing & Tuley 1991; Zuckerman *et al.* 1993). It is this tradition of research that has led to the five-factor model of personality. This model states that the five broad personality dimensions of Extraversion, Neuroticism, Agreeableness, Conscientiousness and Openness to Experience, which capture about 50 per cent of the dispositional variation that is reflected in a variety of languages, are the most robust independent dimensions of human personality that can be identified (Goldberg 1990; Costa & McCrae 1992). Note that these dimensions are rather broad and all encompass various sub-traits (often called 'facets') because they show reliable intercorrelations. For example, Extraversion encompasses traits like sociability, boldness and positive emotionality, while Neuroticism encompasses traits like anxiousness, depressiveness and irritability. An interesting difference between the HPP and BE literatures is that the phenotypic and genetic covariance structure of personality variables in humans has generally been found to be much the same across cultures (Yamagata *et al.* 2006; De Fruyt *et al.* 2009), whereas in BE, different patterns of phenotypic and genetic correlations have been found in different populations (Bell 2005; Dingemans *et al.* 2007, 2009). It is as yet unclear whether this reflects a genuine difference between humans and some other species, or whether the methods used are simply so different in the two cases as to produce different patterns of results.

Whereas BE studies often identify a single personality dimension and explore its consequences in minute detail, HPP typically studies several (e.g. five) personality dimensions at a time in the same sample. HPP has also identified a wider range of different personality constructs overall. Whether this is because of unique characteristics of humans, because human researchers can gather more data about each of their participants (especially when using questionnaires), or simply that the goals of the enterprise tend to be somewhat different, remains to be seen.

Two other findings from the descriptive HPP literature are noteworthy. Firstly, human personality clearly varies along quantitative dimensions. Splitting samples into discrete groups according to their personality is done, if at all, for statistical purposes only, but the underlying distributions indicate continuity. Attempts to use the internal organization of multiple personality dimensions to identify discrete personality types (e.g. neurotic, introverted 'overcontrollers'; unagreeable, unconscientious 'undercontrollers') have been undertaken repeatedly, but it has been found that individuals still vary in how well they represent empirically identified types (Asendorpf 2002). Thus, it can be concluded that personality variation is always best treated as continuously distributed, rather than as categorical types.

Second, HPP has found strong evidence for a high temporal stability of personality, especially of

dispositional ratings, even over several decades (Costa *et al.* 1980; Roberts & DelVecchio 2000). Cross-situation consistency in personality has been more debated. Some of the most cited studies of this question found only very small correlations between, for example, student punctuality and thoroughness in note-taking, even though both of these fall under the umbrella of the dispositional rating 'conscientious' (Mischel 1968). In general, cross-situation consistencies in behaviour are quite modest (though see Funder & Colvin 1991). This has led HPP in two contradictory directions. One response to these data was to abandon very broad, unconditional personality constructs such as 'nervousness' or 'conscientiousness' in favour of more situationally circumscribed ones such as 'nervousness about exams' or 'thoroughness about note-taking'. These narrower constructs have higher intra-individual consistencies (Wright & Mischel 1987). The other response was to maintain the very broad constructs, but to see them as forces whose significance only becomes manifest when one aggregates over many different situations over time. Thus, to call individual A more nervous than individual B is to claim that A's average nervousness across dozens of different situations would be higher than B's, even though in a fair few of those situations, the rank order would be reversed. This formulation reconciles the idea that personality variation is important in the long run with the observation that consistency across any two situations may be quite low.

Behavioural ecologists reading this part of the HPP literature will find aspects of it unfamiliar. First, there is a strong reliance on self-report, and on using people's dispositional descriptions of themselves (or of others) as a basis for claims about actual phenotypic variation. More rarely, act frequencies obtained by direct behavioural observation or recall are used (Buss & Craik 1983), but generally rather little of the personality trait literature involves any direct measurement of behaviour (Furr 2009). Behavioural ecologists might question whether this exercise reveals more about the semantic space of the raters than the behavioural phenotypes of the rated. However, on the other hand, self- or acquaintance ratings do have a number of advantages. People know themselves and their friends from rich experience across a wide variety of different situations, and they implicitly average across these when evaluating statements such as 'I am a nervous person'. Thus, a rating may give a more complete picture than for example behavioural observation in just one situation or on just 1 day. This also means that ratings are likely to 'distil' that component of trait differences which is consistent across situations, making them more general but less predictive of any specific behaviour in a specific situation (Funder & Colvin 1991). Therefore, ratings are also less likely to reflect personality \times environment interactions, unless the environmental component is explicitly built into the rating items (Mischel & Shoda 1995). In support of their reliability, ratings achieve good consistency across individuals and time, especially when aggregated across multiple raters (Costa *et al.* 1980; McCrae & Costa 1987).

Second, the use of the covariance structure of multiple rating dimensions as an arbiter of biological

importance of a trait is different from normal BE practice (ratings and factor analysis are sometimes used in the animal literature, but dispositional rating data are generally considered inferior to behavioural observation; see Gosling 2001; Uher & Asendorpf 2008). Behavioural ecologists are more used to single indices of personality, and to seeing consequences for survival and reproduction as the arbiter of importance. Prolonged, essentially atheoretical debates about whether there are two, three, five or six factors of personality, when the relevance of these factors to life outcomes is as yet undemonstrated, might seem uninspiring to outsiders.

Third, there is a potential source of confusion around the term 'explain'. Personality psychologists will often claim that five factors suffice to 'explain' the important variation in human personality. However, explain here is being used in a particular, statistical sense; there is redundancy in people's self-ratings, such that most of the variance in these ratings can be captured statistically by positing five latent variables, which we label personality traits. It is very common in psychology to posit such latent variables (intelligence is another one), and to talk about them as if they were explanatory, when in fact they arise purely inductively from covariance patterns within data (Borsboom Mellenbergh & van Heerden 2003). They are not explanatory in any of the senses of explanation used within BE; they specify neither the proximate mechanisms nor evolutionary forces lying behind personality variation.

These criticisms of personality trait-identification research have not been lost on personality psychologists either, and trait-identification approaches such as the five-factor model have received searching criticisms for the reasons listed above, among others (McAdams 1992; Block 1995; Mischel & Shoda 1995). These critiques are both cogent, and in another sense, unfair. Trait-identification research sets out to answer descriptive questions at the population level, and as such it is unreasonable to expect it to answer questions of a different kind, such as proximate or ultimate explanatory questions. Given the applied focus of much HPP research, whose goals include providing simple assessment frameworks for personnel or educational selection, the focus on descriptive adequacy of simple questionnaire measures is understandable.

(b) Proximate mechanisms

Questions of proximate mechanism have been addressed within HPP in the *personality processes* tradition of research, which seeks to identify cognitive or motivational underpinnings of individual signatures of behaviour (Mischel & Shoda 1995; Revelle 1995). Recently, theorists have begun to link the trait-identification tradition, specifically the five-factor model of personality, with the *personality processes* tradition, by identifying candidate psychological mechanisms that underlie variation in each of the major traits (Denissen & Penke 2008a,b). Thus, for example, a candidate proximate explanation for individual differences in extraversion is variation in the functioning of mid-brain reward systems (Depue & Collins

1999), whereas a candidate mechanism underlying variation in agreeableness is the availability of theory of mind, which is the capacity or motivation to represent and reason about the mental states of others (Nettle & Liddle 2008). These mechanisms can increasingly be investigated at the physiological, neural and genetic levels (Matthews *et al.* 2009). However, it is important to note that there is no *a priori* reason to assume that any single proximate mechanism matches to any dimension of individual differences in a trait (Borsboom *et al.* 2003; Cervone 2004), which is why researchers should be prepared to find systems of evolved mechanisms relating to trait dimensions (Penke *et al.* 2007a; Penke 2010).

(c) *Genetic and environmental aetiology*

Much work has been done on the quantitative behaviour genetics of human personality. Since BE methods like breeding and cross-fostering experiments are not feasible in humans, studies in this area usually rely on 'natural experiments' like twins or adoption families. Converging evidence shows heritabilities of about 50 per cent for virtually every human personality trait that has been studied, with indications of both additive and non-additive genetic variance as well as environmental influences that are mostly not shared among family members (Penke *et al.* 2007a; Johnson *et al.* 2008). There is also evidence that the additive genetic correlations underlying the five-factor model (i.e. the G matrix of human personality) resemble the phenotypic correlation matrix very well and are robust across different populations (Yamagata *et al.* 2006). However, gene \times environment interactions and gene-environment correlations have not been modelled very often in studies of human personality, even though the necessary statistical methods exist, and their effects might be hidden in the additive genes-plus-environment models more commonly applied (Johnson 2007). This might be a critical neglect, since humans have a strong tendency to select, construct and adapt to their own environmental niches (Buss 1987; Penke 2010). Indeed, transactional relationships between personality and environment have a prominent status in the personality development literature (Roberts & Pomerantz 2004).

(d) *Fitness consequences*

The question why natural selection would have maintained intra-population variability on personality dimension has only recently received attention within HPP (Buss 1991, 2009; Buss & Greiling 1999; Nettle 2006; Penke *et al.* 2007a,b; Penke 2010). In part, this reflects the more general growth in evolutionary thinking in psychology since the early 1990s, and in part it reflects a direct influence of the BE personality work on human research, with the work of Dingemans *et al.* (2004), for example, clearly having an impact on our papers (Nettle 2006; Penke *et al.* 2007a,b). However, personality traits are known to predict a myriad of life outcomes related to survival, reproduction and parental investment that must be regarded as components of fitness (see below).

(e) *Comparative personality research*

The phylogenetic perspective has been largely neglected so far in HPP, though some attempts have been made to apply the descriptive methodology of HPP to non-human species (Gosling 2001; Uher 2008; Weiss & Adams *in press*). Also, functional equivalents of candidate genes that have been implied in studies of human personality (like *DRD4*, *5-HTTLPR* and *MAOA*; Ebstein 2006) have been successfully associated with similar behavioural phenotypes in species such as macaques (Wendland *et al.* 2005) and great tits (Fidler *et al.* 2007; Korsten *et al.* 2010), suggesting at least some phylogenetic continuity.

Finally, it should be noted that HPP pursues some additional objectives that might be rather unfamiliar to BE. For example, phenomenological personality research asks how individuals make sense of their own motivations and dispositions, and how they achieve a sense of coherence and organization through time. Such questions arise most obviously in a self-conscious, self-reflective linguistic species such as humans. They are thus not generally considered within BE, though they receive considerable attention with HPP (see McAdams 1996).

3. OUTSTANDING ISSUES WITH HUMAN PERSONALITY PSYCHOLOGY

Having briefly outlined above some of the concerns of HPP research, in this section we discuss some of the outstanding questions. In particular, we wish to suggest that ideas and techniques developed in the BE personality literature are often convergent with, or useful to, some of the most promising ideas within HPP. We can thus look forward to a greater conceptual unification of the two areas in future.

(a) *What is a personality trait?*

The question of what is a personality trait is an apparently simple one, but nonetheless one that has been the subject of intense discussion in HPP over the years. In the simplest terms, a personality trait is simply the tendency of an individual to behave in a certain way. However, this immediately evokes the observation that the situation the person is in is often a more important predictor of their behaviour than their personality characteristics are, which has led to prolonged debate about the relative importance of dispositional and situational determinants of behaviour (see Funder 2006). A more sophisticated view of personality traits thus sees them as a hypothesis about the *interaction* of a person and a situation; that is, to be high on trait X is to respond in a certain way to situations of class Y. There is plenty of evidence for this view; people high in neuroticism have a greater physiological response to a stress challenge than people low in neuroticism (Schneider 2004) and are more sensitive to signs of social rejection (Denissen & Penke 2008b); people high in extraversion respond to funny film clips or positive pictures more strongly than people low in extraversion (Gross *et al.* 1998). For each major personality trait, it is possible to identify a natural class of situations to which the affective or behavioural response is predicted by that personality score.

To make this view more precise still, the concept of reaction norm, which comes from biology, is useful (van Oers *et al.* 2005; Denissen & Penke 2008a; Dingemanse *et al.* 2010). A reaction norm is a function describing the relationship between environmental input and phenotypic output. Thus, to have a certain level of a particular personality trait is to have a particular shape of reaction norm to the relevant class of situational cues. A particularly useful consequence of thinking in terms of reaction norms is that it leads us to realize that individuals might differ in terms of the elevation of their reaction norm (that is, their level of a certain behaviour in the average situation), or its slope (that is, the degree to which their levels of behaviour change as the situation changes). These two possibilities have sometimes been distinguished within HPP research (Gross *et al.* 1998), but not consistently so, and personality traits are sometimes thought of as differences in the average level of behaviour, and sometimes in terms of magnitude of response to a class of cue. The behavioural reaction norm perspective clarifies this issue. Note that Dingemanse *et al.* (2010) suggest referring to elevation differences as ‘personality’ and to slope differences as ‘plasticity’, while ‘personality’ in HPP generally refers to stable individual differences in either elevation, slope or both. We feel that the distinction between elevation and slope is a useful one, but note that there is potential for misunderstanding between the two subfields to the extent that they apply the term ‘personality’ slightly differently in this regard. A possible solution would be to establish the terms ‘personality elevation’ (or ‘average personality’) and ‘personality plasticity’ in both disciplines.

Reaction norm thinking also helps to clarify what the scientific status of a personality trait is. As mentioned above, personality traits like extraversion are, within HPP, sometimes proffered as explanations of behaviour, and sometimes as mere descriptions of behaviour. In other words, they seem sometimes to be the *explanans*, and sometimes the *explanandum*. If they are in fact reaction norms, then this ambiguity becomes easy to defuse. Personality traits are intermediate level constructs, which summarize the slope and intercept of individual responses to classes of environmental input, and thus make predictions at the individual level. Thus, in one sense, they can be the *explanans* of individual behaviour. However, at the deeper level, they are an *explanandum*; what processes, both proximate and ultimate, account for individuals having the reaction norms that they do? These kinds of questions have been successfully addressed within BE, and a greater understanding of the BE results will help psychologists achieve greater explanatory depth in their work.

(b) *Are ratings valid?*

As mentioned above, one question a behavioural ecologist might have about HPP research is whether verbal ratings actually capture important phenotypic variation. This question is acute, since measurement of actual behaviour is somewhat neglected in contemporary psychology (Baumeister *et al.* 2007;

Furr 2009). However, there are two approaches to validating rating data which help respond to this question. One is to examine the correlations between rated dispositional qualities, and direct behavioural observation in relevant situations over short time periods. Such research has been done surprisingly rarely, but the results show significant and comprehensible associations between rated traits and actual behaviour (Vazire & Mehl 2008; Back *et al.* 2009). A second approach is to examine the long-term predictive power of personality ratings for fitness-related and thus biologically important outcomes such as survival, social status, mating and reproductive success (Ozer & Benet-Martinez 2006; Roberts *et al.* 2007; Jokela *et al.* 2009, 2010; Weiss *et al.* 2009). Studies of this kind have appeared only recently, but generally support the predictive utility of rating-based personality assessment. The most convincing studies are prospective and longitudinal (e.g. Kelly & Conley 1987; Friedman *et al.* 1995; Soldz & Vaillant 1999; Lee *et al.* 2006; Shipley *et al.* 2007; Deary *et al.* 2008).

(c) *How important are personality differences?*

As mentioned above, HPP research has sometimes been preoccupied with debate about what the relative importance of personal and situational variables is. The answer is clearly that personality becomes important when the situation is constant, or behaviour is aggregated across many situations. However, just how important? Psychologists have not developed a natural framework for quantifying the importance of a variable to real life, but BE provides such a framework by leading us to ask what the strength of the impact on reproductive success is. This impact can be quantified in the form of a standardized selection gradient (Kingsolver *et al.* 2001), and Nettle & Pollet (2008) introduced the use of such gradients as a measure of the importance of different variables in human data. Since personality clearly impacts on reproductive outcomes (Jokela *et al.* 2009, 2010), we thus have a potential framework for assessing the magnitude of its life importance compared with other factors, such as intelligence or socioeconomic status. However, it is worth noting that if selection acts in a negative frequency-dependent or otherwise spatio-temporally fluctuating manner, then there may be no selection apparent from measuring the population-wide association between personality and reproductive success, even if personality is in fact highly consequential.

Personality may be more important than is immediately apparent, because the personality variables, as well as predicting the response to environmental circumstances, predict which environmental circumstances an individual will experience, since individuals with certain dispositions will seek out certain niches or interactions within their overall habitat. This has long been recognized within HPP (Buss 1987; Saudino *et al.* 1997), and is increasingly recognized in BE (see Dingemanse *et al.* 2010). Researchers have also shown that major life events in humans show substantial heritability (Bemmels *et al.* 2008), suggesting that influences of personality variables on situational experience are ubiquitous.

4. CONCLUSIONS

We have discussed two rather different traditions of research into individual differences, HPP and BE, which have evolved largely independently and been motivated by rather different concerns. HPP research starts from the obvious fact that individuals are rather different from one another, and its original concerns were descriptive and often applied, in spheres such as assessment for industry or education. BE research started from the postulate that the situation is the overwhelming determinant of adaptive behaviour, and thus that animals facing the same situation should behave in the same way. Its interest in personality began with the observation that this is often not the case.

Despite these very different beginnings, and different methodological traditions, we see strong potential for convergence between these two areas in the coming years. The need for validation of ratings against actual behaviour will point psychologists to BE methods of measuring behaviour, especially since HPP lacks an equally well-developed descriptive structure for human behaviours and relevant situations as there is for personality (Funder 2006), something for which an evolutionarily informed approach is probably invaluable (Uher 2008). Also, the increasing concern within HPP with the long-term life importance (as opposed to the short-term psychometric properties) of our constructs naturally leads us to examine the BE tradition of measuring consequences of phenotypic characters for survival and reproductive success. Ultimately, this might lead HPP to accept that personality traits are best conceptualized as behavioural reaction norms that, while possibly relying on diverse genetic, physiological and neuronal substrates, serve a common goal in that they help individuals to adapt to specific aspects of their environments (Penke *et al.* 2007a; Matthews *et al.* 2009).

Finally, behavioural ecologists may find much of interest within the HPP literature. Psychologists have a hundred years experience of documenting the structure of phenotypic variation, and relating this to psychological processes that differ between individuals. Methodological advances in HPP could help behavioural ecologists to develop equally comprehensive personality profiles of other species (Uher 2008; Weiss & Adams *in press*). For humans, the result of this has been the observation that behavioural phenotypes vary continuously along several recurrent axes, which relate to major classes of motivations (Denissen & Penke 2008a), are temporally stable and significant to life outcomes, and are influenced by both genetic and environmental factors. This converges with the increasingly influential view within BE that differences between individuals within the same population are both substantial and important.

L.P. is funded by the UK Medical Research Council (grant no. 82800), which is part of the Help The Aged-funded Disconnected Mind research programme. The work was partly undertaken at The University of Edinburgh Center for Cognitive Ageing and Cognitive Epidemiology, part of the cross-council Lifelong Health and Wellbeing Initiative. Funding from the BBSRC, EPSRC, ESRC and MRC is gratefully acknowledged.

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