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Research highlights

Interactions between attention and visual short-term memory (VSTM): What can be learnt from individual and developmental differences?

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Duncan E. Astle, Gaia Scerif*

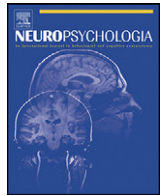
► Attentional control abilities predict individual differences in VSTM capacity. ► Developmental increases in capacity are associated with fronto-parietal changes. ► The neural circuitry underlying VSTM capacity changes may be modified by training. ► The developmental and adult cognitive neuroscience of VSTM inform one another.



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Interactions between attention and visual short-term memory (VSTM): What can be learnt from individual and developmental differences?

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ABSTRACT

An ever increasing amount of research in the fields of developmental psychology and adult cognitive neuroscience explores attentional control as a driver of visual short-term and working memory capacity limits (“VSTM” and “VWM”, respectively). However, these literatures have thus far been disparate: they use different measures or different labels, and the constructs of interest often appear to be quite distinct. In the current review, we attempt to bridge these gaps across disciplines and explore the extent to which these two literatures might support one another. In order to do this, we explore five principal questions of interest to members of both communities: (1) To what extent are measures of VSTM, VWM and attentional control commensurate across the developmental and adult literatures? (2) To what extent do individual differences in attentional control account for why some children, just like some adults, show poorer VSTM and VWM capacity than others? (3) Can developmental improvements in VSTM and VWM capacity also be explained by differences in attentional control? (4) What novel insights can be gained by studying the developmental cognitive neuroscience of attention and VSTM and VWM? (5) Can visual short-term and working memory capacity be modulated by training and, if so, how can training effects inform the relationships between attention and VSTM? Throughout, we evaluate the central thesis that variability in attentional control, both between individuals and over development, is a driver of variability in VSTM and VWM capacity.

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The ability to hold in mind previously seen information for brief periods of time is essential to many cognitive and perceptual processes. This is typically referred to as visual short-term term (“VSTM” henceforth), the process of maintaining previously seen information in a privileged state of activation. Maintenance is sometimes, but not always, required to be performed at the same time as a secondary task, in which case it is referred to as visual working memory (“VWM” henceforth). The distinction between VSTM and VWM, i.e., between ‘maintenance’ and ‘maintenance plus storage’, is particularly important and not necessarily equivalent across the developmental and adult literatures; the first section of this review therefore deals with it in depth. As the human brain develops, it becomes capable of maintaining more items in this privileged state—that is, VSTM and VWM capacity increase greatly with age, however one defines them. There exist a number of excellent reviews that chart various aspects of this development: Gathercole (1999) and Pickering (2001) review the development of

primarily verbal and visual working memory capacity, respectively, through childhood and adolescence; Klingberg (2006) focuses on the development of a superior frontal-intraparietal network and its relationship to developmental increases in VSTM capacity. Furthermore, the amount of visual information that can be held in mind is also known to differ greatly across individuals of the same age (see Conway, Jarrold, Kane, Miyake, & Towse, 2007, for an excellent review on this topic). These differences, both across individuals and developmental time, are particularly important in childhood, when they significantly predict academic success. The ability to hold in mind pieces of task-relevant information is likely to be critical for learning new skills, solving novel tasks and acquiring new knowledge (e.g., Alloway & Alloway, 2010; Alloway, Gathercole, Willis, & Adams, 2004; Gathercole & Pickering, 2000; Gathercole, Pickering, Knight, & Stegmann, 2004; Gathercole, Service, Hitch, Adams, & Martin, 1999). Of note, these relationships have been more extensively studied in the context of verbal rather than visual information, but recent evidence also suggests a role for VSTM and VWM in predicting academic outcome. For example, Bull and colleagues (Bull, Espy, & Wiebe, 2008) found that VSTM span (measured in the forward Corsi Blocks task) in a group of children aged 4(1/2) years significantly predicted mathematics but not reading outcome when children were re-assessed over the first three pri-

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58 mary school years. Visual WM (backwards Corsi Blocks span) also
59 related to mathematics at all time points. We shall return to the dis-
60 tinction between VSTM and VWM in due course, but for now the
61 existing corpus of evidence suggests that not only does a child's
62 current working memory capacity predict their concurrent per-
63 formance on a range of academic measures (e.g., Bull & Scerif,
64 2001; Gathercole, Pickering, Knight et al., 2004; St Clair-Thompson
65 & Gathercole, 2006), but their current working memory perfor-
66 mance predicts their future academic performance (Bull et al.,
67 2008; Gathercole, Tiffany, Briscoe, Thorn, & team, 2005). Indeed,
68 over 80% of children with low working-memory capacity (those
69 falling in the bottom 10th percentile for their age) have signifi-
70 cant problems with reading or mathematics, and usually with both
71 (Gathercole & Pickering, 2000).

72 Alongside the literature on the development of working mem-
73 ory and its educational outcomes, cognitive neuroscientists have
74 recently focused on potential neurocognitive factors limiting
75 VSTM capacity in adults (e.g., Luck & Vogel, 1997; McCollough,
76 Machizawa, & Vogel, 2007; Vogel & Machizawa, 2004; Vogel,
77 McCollough, & Machizawa, 2005). More specifically, given the vast
78 amount of visual information competing to gain access to this
79 privileged form of short-term maintenance, the ability to select
80 appropriately what ought to be stored and ought to be ignored
81 has been proposed to be intimately intertwined with measures
82 of VSTM capacity (Cowan & Morey, 2006; Fukuda & Vogel, 2009;
83 Kane, Bleckley, Conway, & Engle, 2001; Vogel & Awh, 2008; Vogel &
84 Machizawa, 2004; Vogel et al., 2005). However, with a few notable
85 exceptions (Cowan et al., 2005; Cowan, Fristoe, Elliott, Brunner,
86 Q1 & Saults, 2006; Cowan, Morey, AuBuchon, Zwilling, & Gilchrist;
87 Cowan, Naveh-Benjamin, Kilb, & Saults, 2006), the majority of
88 accounts of the specific relationships between attentional control
89 and VSTM focus on its mechanisms in adulthood, without consid-
90 ering the maturation process that both of these mechanisms likely
91 undergo, or indeed whether the same processes accounting for
92 VSTM capacity hold across development, rather than just in adult-
93 hood. And yet, discovering what factors limit changes in VSTM or
94 VWM capacity over development can constrain their role in adult
95 models (Cowan, 2004). For instance, if developmental changes in
96 VSTM or VWM capacity are driven by the scope (or amount) of
97 information that can be attended at each moment in time, this
98 parameter may also constrain adult limits (Cowan, Fristoe et al.,
99 2006). In turn, if VSTM or VWM limitations primarily stem from
100 processing speed problems (e.g., Kail & Salthouse, 1994; but cf.
101 Cowan, Elliott et al., 2006), then we would expect the development
102 of capacity to track the development of speed of processing closely.
103 Alternatively, if one conceives of the basic limit to VSTM/VWM
104 development as being essentially attentional (i.e., either the ability
105 to gate what gains access to storage, or to bias what is already held
106 in memory, as suggested by Fukuda & Vogel, 2009; Vogel et al.,
107 2005), then these basic attentional limits may also contribute to
108 adult VSTM/VWM capacity limits.

109 With these two distinct strands of work in mind, five related
110 questions arise. First, are measures of VSTM, VWM and attention,
111 and the constructs that they are imputed to tap, equivalent across
112 these two literatures? Second, what accounts for some children's
113 poorer VSTM/VWM capacity? Third, and beyond a focus on individ-
114 ual differences, what factors underpin the increase in VSTM/VWM
115 capacity over developmental time? Fourth, what insights can be
116 gleaned from studying the neural correlates of individual and age-
117 related differences in VSTM/VWM? Fifth and final, how can training
118 studies in children inform theories of the relationships between
119 attentional control and VSTM? The current review evaluates criti-
120 cally the potential role of attentional control in addressing these
121 issues.

122 First, we tackle head-on critical differences in terminology and
123 constructs referring to attentional control and visual short-term

memory in the developmental and adult cognitive neuroscience
literature. We indeed believe that it is critical to evaluate whether
these two fields collect commensurable information, and, if not,
what steps need to be followed to integrate these approaches.

1. Attention and VSTM/VWM for developmental psychologists and cognitive neuroscientists: commensurable constructs and measures?

To begin with definitions of visual attention, the developmental
literature on this topic has stressed differences across related but
relatively distinct attentional processes, such as sustained atten-
tion (the ability to maintain one's task goal over a period of time),
selective attention (i.e., the ability to select task-relevant loca-
tions or objects amongst irrelevant distractor items), and executive
attention/attentional control (i.e., the ability to control stimulus-
response conflict associated with target stimuli and potentially
relevant distractor locations, objects or tasks) (e.g., Colombo, 2001;
Manly et al., 2001; Rueda et al., 2004). The great weight placed
on independence across attentional processes was driven by adult
cognitive neuroscience models focused on distinct attentional neu-
ral networks (e.g., Fan, McCandliss, Sommer, Raz, & Posner, 2002;
Posner, 1980; Posner & Cohen, 1984; Posner & Rothbart, 2007), but
it contrasts with the parallel and also growing cognitive neuro-
science emphasis on construing attentional processes as unified
biasing mechanisms that perhaps operate to enhance task-relevant
stimuli/dimensions and suppress irrelevant materials, very simi-
larly albeit at different processing stages (e.g., incoming perceptual
input, information held in memory) and tasks (e.g., selecting stim-
uli in space, as opposed to specific responses) (Desimone & Duncan,
1995; Kastner & Ungerleider, 2000; Mesulam, 1999). Here, and con-
sonant with the latter set of cognitive neuroscience models, by
'visual attention', we refer to the ability to apply top-down con-
trol in order to bias either incoming visual input, or information
already held in short-term storage, according to which of its aspects
are relevant to the task at hand.

Regardless of the stress on either common mechanisms or inde-
pendence of processes, taxonomies of attention development have
not drawn explicit implications of developmental changes in atten-
tional control for short-term memory maintenance, as the majority
of tasks employed to tap attentional processes in children are
simple target detection or discrimination tasks. For example, devel-
opmental changes in children's ability to select visual stimuli have
been extensively studied by contrasting target detection and dis-
crimination at cued and uncued locations (Akhtar & Enns, 1989;
Brodeur & Boden, 2000; Brodeur & Enns, 1997; Goldberg, Maurer,
& Lewis, 2001; Iarocci, Enns, Randolph, & Burack, 2009; Ristic &
Kingstone, 2009; Wainwright & Bryson, 2002, 2005) using the clas-
sical Posner cueing paradigm (Posner, 1980; Posner & Cohen, 1984),
but not (until recently, see Astle, Nobre, & Scerif, 2010) memory
for items at such locations. However, all models of developmen-
tal changes in attentional processes predict relationships with
changing memory abilities. For example, thinking of attention as
sustained maintenance over time might suggest a close relationship
between developmental changes in attention and memory, because
memory is required to maintain a task goal over a prolonged period
of time, although there is no reason to believe that such a relation-
ship would be specific to visual memory, and not extend to verbal
working memory. Similarly, developmental changes in selective
attention may drive changes in memory, because selection can
bias sensory input according to what ought to be maintained in
short-term or working memory, or even bias those representa-
tions once stored (Griffin & Nobre, 2003; Nobre et al., 2004; Nobre,
Griffin, & Rao, 2008). Indeed, a substantial part of the literature on
working memory development has construed attentional control

187 as the co-ordination and rehearsal of to-be-remembered mate-
188 rials, “the central executive” (Baddeley, 1996; Baddeley & Hitch,
189 1974; Gathercole, Pickering, Ambridge, & Wearing, 2004; Hitch &
190 Halliday, 1983; Hitch, Halliday, & Littler, 1989), but, by definition,
191 this work focuses more on higher-level modality-general aspects
192 of attentional control, which likely combine many separable mech-
193 anisms, and less on how these processes may directly modulate
194 lower-level visual processing (in both cognitive and especially neu-
195 ral terms). So, much remains to be learnt from bridging models of
196 attentional control in adult cognitive neuroscience and the role of
197 attentional control in VSTM and VWM over developmental time.

198 Even more problematic, the precise operationalisation of visual
199 short-term memory itself varies greatly across the developmen-
200 tal and cognitive neuroscience literature. Whilst VSTM and VWM
201 are used relatively interchangeably in the adult cognitive neuro-
202 science literature to index maintenance in the absence of visual
203 input (Corbetta, Kincade, & Shulman, 2002; Courtney, Ungerleider,
204 Keil, & Haxby, 1997; Todd & Marois, 2004), the same is not true of
205 work on developmental changes in memory capacity, as we detail
206 below. In addition, the measures employed to tap these constructs
207 are not always comparable. For example, in the adult cognitive neu-
208 roscience literature, Cowan’s K is defined as the capacity measure
209 of choice for VSTM/VM studies (e.g., Todd & Marois, 2004; Vogel
210 & Machizawa, 2004; Xu & Chun, 2006). Participants are presented
211 with various set-sizes of to-be-remembered stimuli (for instance
212 coloured squares) and after a delay those stimuli are re-presented.
213 On half of all trials one of the stimuli will change (for instance a
214 change in colour) and participants’ task is to identify those trials
215 upon which a change has occurred. K is calculated as the proportion
216 of correct hits minus the proportion of false alarms, multiplied by
217 the set-size (Cowan, 2001). In adults, K is usually at or around four,
218 implying that VSTM (a.k.a. VWM) has a processing limit of around
219 four pieces of information, or ‘objects’. The extent to which this
220 object-based capacity limit is dependent on the complexity of each
221 object is highly debated (Luck & Vogel, 1997; Vogel, Woodman, &
222 Luck, 2001; Wheeler & Treisman, 2002). There has been a great deal
223 of interest in the neural mechanisms that underpin this capacity
224 limit and on the nature of the limit itself (e.g., Bays & Husain, 2008,
225 2009; Cowan & Rouder, 2009; Fukuda, Awh, & Vogel, 2010).

226 In contrast, in the developmental literature K is more rarely used
227 as a measure of capacity limits (cf. Astle & Scerif, in preparation;
228 Cowan et al., 2005; Cowan, Fristoe et al., 2006; Cowan, Naveh-
229 Benjamin et al., 2006; Riggs, McTaggart, Simpson, & Freeman,
230 2006). Amongst the few exceptions, Riggs et al. (2006) found that
231 K ranged from 1.52 items for 5-year-olds, 2.89 items for 7-year-
232 olds, and 3.83 items for 10-year-olds. In a study to which we later
233 return, we measured K in a group of 6–7 year old children and
234 have observed K estimates of around 2.5 items (Astle & Scerif, in
235 preparation), i.e., in both cases substantially lower than the figures
236 reported on average for adults. Studies like these notwithstanding,
237 visual short-term and working memory capacity limits in children
238 are typically measured using *span* tasks. Children are presented
239 with a list of to-be-remembered locations (which increases until
240 performance drops to a pre-established threshold), these are either
241 retrieved at the end of the trial verbatim, or they are to be main-
242 tained alongside a requirement for concurrent processing (as for
243 example mental rotation) and/or somehow manipulated prior to
244 retrieval (as reporting the sequence backwards). Termed simple
245 and complex memory span tasks, respectively, these are viewed
246 quite differently in the developmental literature. The former would
247 be typically described as visuo-spatial *short-term* memory and the
248 latter as visuo-spatial *working* memory. Complex span is typically
249 seen as the gold-standard in verbal and visual working memory
250 measures, and the best predictors of subsequent academic achieve-
251 ment, although some researchers do emphasise a role for span
252 tasks without concurrent processing requirements as good indices

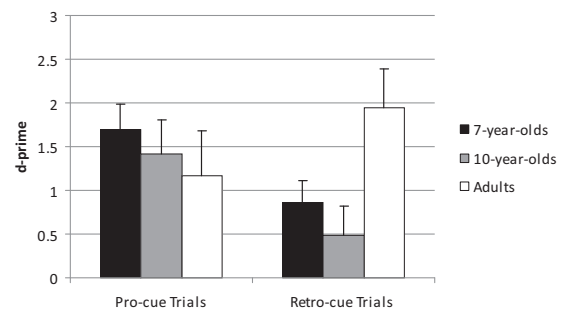


Fig. 1. Mean D-prime benefits following pro-cues and retro-cues for 7-year-olds, 10-year-olds and adults. Benefits were calculated as the difference in d-prime scores between cued trials and neutral trials. Error bars indicate the standard error of the mean (Adapted from Astle et al., 2010).

253 of working memory and of outcome (see Cowan et al., 2005, for a
254 comprehensive review of arguments for and against complex span
255 measures). One potentially important difference between complex
256 and simple span tasks is the extent to which top-down attentional
257 control is required. Complex memory span tasks, which are thought
258 to recruit attentional control in addition to storage, are more closely
259 associated with reasoning ability and fluid intelligence (Conway
260 et al., 2007; Conway, Kane, & Engle, 2003; Kane & Engle, 2002).
261 It is worth noting that in children even simple span tasks may
262 recruit substantial attentional resources, and thus, the concepts of
263 visual-spatial *short-term* memory and visuo-spatial *working mem-
264 ory* blur differentially depending on the age of the individuals being
265 assessed. This has been very clearly illustrated in the case of verbal
266 short-term and working memory by performance on the backward
267 digit span task, as the latter measure loads with other measures
268 of verbal working memory span in children, but verbal short-
269 term memory span in adults (St Clair-Thompson, 2010). A further
270 distinction to note between the developmental and the adult lit-
271 eratures is the extent to which traditional span tasks, compared to
272 the change detection tasks used in the adult literature, involve both
273 visual and spatial components: now classical developmental stud-
274 ies of visuo-spatial memory distinguish between visual and spatial
275 information (e.g., Hitch, Halliday, Schaafstal, & Schraagen, 1988;
276 Logie, 2003; Logie & Pearson, 1997; Pickering, 2001), whereas the
277 adult cognitive neuroscience literature does not always differen-
278 tiate across them (but see Courtney et al., 1997; McCarthy et al.,
279 1996; for exceptions).

280 A possible way of unifying these seemingly disparate fields
281 would be for researchers to adopt tasks that are commonly used
282 across both strands of research and assess how they relate. For
283 instance, Posner’s classical spatial cueing paradigm has often been
284 used with children (Akhtar & Enns, 1989; Brodeur & Boden, 2000;
285 Brodeur & Enns, 1997; Goldberg et al., 2001; Iarocci et al., 2009;
286 Ristic & Kingstone, 2009; Wainwright & Bryson, 2002, 2005), but
287 not in function of studying the impact of visual selection on visual
288 memory. We presented spatial cues in advance of (pro-cue tri-
289 als), or following (retro-cue trials), four to-be-remembered objects
290 (Astle et al., 2010). At the end of each trial a probe object appeared,
291 and that the child’s task was to decide whether or not it was one
292 of the original four. Unsurprisingly, performance for both adults
293 and children (aged 6–11 years) improved dramatically with a pro-
294 cue: when attention biased one of the items at encoding it was
295 subsequently better recognised. However, whilst adults’ perfor-
296 mance benefited just as much from a retro-cue, children drew only
297 marginal benefit from a retro-cue, suggesting that using attention
298 to bias an object in VSTM has a slower developmental trajectory
299 than attentional biases on encoding (see Fig. 1).

300 Furthermore, in children individual differences in retro-cue
301 benefit (performance on valid retro-cue minus neutral-cue trials)

significantly predicted variance in simple and complex visuo-spatial, but not verbal, span tasks—i.e., those children with the best visuo-spatial short-term and working memory scores were the ones best able to bias their VSTM with spatial attention. We believe that it is by using tasks commonly used with adult populations (Griffin & Nobre, 2003; Nobre et al., 2004, 2008), alongside measures traditionally used with children (e.g., Alloway, 2007; Gathercole, Pickering, Ambridge et al., 2004), such as the spatial span task, that we can begin to bridge the gap between the two literatures. We now turn to the insights gained from studying these individual differences in childhood.

2. The relationship between individual differences in attentional control and VSTM/VWM in children

The ability to bias perceptual representations with spatial or feature-based attention has frequently been related to individual differences in VSTM capacity in the adult literature. For instance, using an electrophysiological index of object storage (e.g., Ikkai, McCollough, & Vogel, 2010; Klaver et al., 2005; McCollough et al., 2007; Vogel & Machizawa, 2004; Vogel et al., 2005) Vogel and colleagues have argued that those with low visual short-term memory capacity, as measured using K, are increasingly likely to store to-be-ignored items. They have also demonstrated that those with low VSTM capacity are more likely to have their attention drawn away from a central rapid serial visual presentation (RSVP) stream (in which they are required to monitor for infrequent targets of a certain colour) by to-be-ignored items that share the target's colour and appear in a neighbouring RSVP stream (Fukuda & Vogel, 2009). Of note, this task does not have any explicit working memory requirements, but attentional capture effects in performance discriminate between individuals with high and low VSTM capacity. In the adult literature there seems to be growing consensus that poor attentional control might constrain VSTM capacity. The study by Fukuda and Vogel is an important one in making this argument: one obvious criticism is that the same pattern of effects would be expected if the reverse relationship were true – VSTM is likely required in attentional selection tasks. However, if this were the case, then we would expect a reduced contingent-attentional capture effect in those with poor VSTM: if these subjects cannot remember what colour target item to monitor for, then they ought to show less of an attentional blink effect when an item of that colour appears in the neighbouring irrelevant stream. Moreover, it also seems unlikely that those with low VSTM have a general problem remembering their goal—were this the case then we ought to see a similar capture effect for items of any colour, not just those in the target colour, appearing in neighbouring streams.

It is not clear whether the relationship observed in adults between overriding attentional capture and VSTM capacity holds true for children, although data from children with Attention Deficit Hyperactivity Disorder (ADHD) suggests their increased distraction from irrelevant singletons at to-be-ignored locations (Mason, Humphreys, & Kent, 2005) and, interestingly, their cognitive profile has been shown to overlap with that of children with low working memory capacity (Alloway, Gathercole, Kirkwood, & Elliott, 2009; Gathercole et al., 2008). We reasoned that, if low visuo-spatial short-term and working memory capacity in children is underpinned by an inability to prevent irrelevant information from capturing attention, then an attentional capture paradigm ought to relate to these capacity measures even more directly than attentional cueing measures in the context of memory (e.g., Astle et al., 2010), as individual differences in the latter may depend on a host of other factors, such as baseline memory abilities. In a recent study we attempted to measure more precisely the ability to select task-relevant items and ignore irrelevant items (Astle & Scerif, in

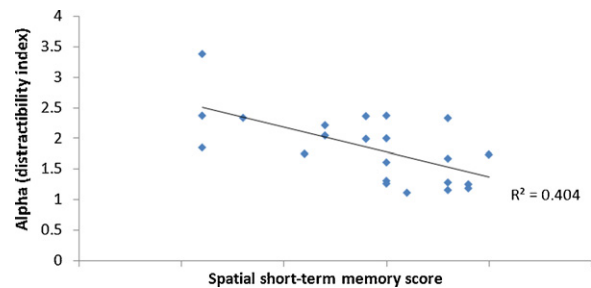


Fig. 2. Relationship between the attentional filtering parameter alpha, a measure of distractibility (y-axis) and visual spatial span score in a sample of 6–7 year-olds (Astle and Scerif, in preparation).

preparation). A group of 6–7 year olds performed a task inspired by Bundesen's theory of visual attention (Bundesen, 1990, 1998; Bundesen, Habekost, & Kyllingsbaek, 2005; Duncan et al., 1999; Peers et al., 2002). We presented the children with arrays of familiar shapes, either containing four targets (4T, e.g., four white shapes), two targets (2T, e.g., two white shapes) or two targets with two distracters (2T2D, e.g., two white shapes and two black shapes). The child's task was to report the identity of target shapes immediately after their presentation. If children were perfect at filtering out distracters, and only allow targets to be retained, performance on the 2T and the 2T2D condition would be equivalent. If they had a poor ability to apply top-down control, and distracters were treated as targets, then performance on the 2T2D and 4T conditions would be equivalent. Performance on the 2T2D condition, by comparison with performance on the 4T and 2T conditions, thus enabled us to estimate each child's filtering ability, termed here ' α ' (see also Duncan et al., 1999; Peers et al., 2002). The lower the α value, the better the child had ignored the distracters; the higher the α value, the greater the distracters had been attended, at the expense of the target shapes. There was a significant relationship between visuo-spatial working memory (spatial span) and α [$r = -0.636$, $p = 0.001$] (see Fig. 2). The better children were at filtering-out distracters, the higher their visuo-spatial working memory capacity, even when controlling for basic speed of processing differences. Interestingly, there was no such relationship with measures of K or standardised measures of visual short-term memory. In addition, this relationship was not present between α and verbal working memory capacity, indicating that the relationship between α and working memory capacity was domain-specific, and that it only related to complex span performance, not simple span or K measures. The most likely reason for the specificity of the relationship is that spatial working-memory tasks hinge on children's ability to avoid being overly distracted by the secondary processing task and thus avoid forgetting the to-be-remembered spatial locations.

In summary, despite VSTM measures being difficult to equate across adult cognitive neuroscience and developmental studies, similar relationships between individual differences in attentional control and VSTM memory seem to exist. Despite differences in absolute capacity between children and adults, individual differences in capacity in any age group can tell us something very important about the nature of the limit itself. In addition, children present ideal candidates for the study of individual differences for a number of reasons: (i) whilst adults tend to develop sophisticated strategies to mask limitations in capacity, children rarely do (e.g., Cowan, Saults, & Morey, 2006); (ii) in most university contexts it is particularly difficult to obtain large variability in capacity, whereas in most schools one can find the full range of low and high working memory abilities; and (iii) these individual differences appear to have important consequences during development, making understanding their origins particularly worthwhile.

3. Explaining developmental improvements in VSTM/working memory capacity with neurocognitive improvements in attentional control

Having examined the state of the current evidence on whether individual differences in VSTM capacity in children can be predicted by individual differences in attentional control, a further question is whether or not *developmental* improvements in attentional control drive *developmental* improvements in VSTM capacity. Whether we use the more basic change-detection VSTM paradigms typically employed in the adult literature (e.g., Cowan et al., 2005; Cowan, Naveh-Benjamin et al., 2006; Riggs et al., 2006), or complex working memory span tasks more typically used with children (e.g., Case, Kurland, & Goldberg, 1982; Daneman & Carpenter, 1980), there are substantial improvements in span through childhood and adolescence, and these improvements could be driven by improvements in capacity per se. For instance, an increase in the ability to use distinctive neural codes to represent different items may result in an improved ability to store more individual objects without those representations overlapping. An alternative and not mutually exclusive driver of change, similar to the proposal for individual differences in capacity, could be an improving ability to bias information that ought to be stored relative to those distracters that ought to be ignored.

There are various approaches to charting developmental improvements in visual short-term and visual working memory capacity. Probably the most influential is a multi-componential approach, which is based on the premise that working memory performance relies on the interplay between relatively discreet sub-components (Baddeley, 1996; Baddeley & Hitch, 1974). It views effective working memory performance as the interaction between (probably heterogeneous) domain general active attentional resources and other domain-specific passive stores. Using tasks that tap these different components of the working memory system, one can explore the rate at which different aspects of working memory develop. Latent factor analysis has been used to assess the relative contribution of underlying factors to performance on the various span-based verbal and visuo-spatial short-term and working memory tasks. The results reliably advocate a three-factor account, similar to that initially posited by Baddeley and colleagues (Gathercole, Pickering, Ambridge et al., 2004): tasks requiring the simple maintenance of visual or verbal information load onto two separate stores, which presumably index underlying passive stores for these two different types of information; tasks requiring the maintenance and concurrent manipulation of information load onto one passive store (depending upon whether they require the maintenance of visual or verbal information) and a mystery third factor. This third factor presumably indexes a supervisory attentional control mechanism (or series of mechanisms). Importantly, this three-factor account provides the best fit for variability across a wide battery of tasks from age 4 through to adulthood and this architecture is largely in place by the start of formal schooling.

The potential reasons for developmental increases in working memory capacity have been traditionally and extensively explored in the verbal domain (e.g., Barrouillet, Gavens, Vergauwe, Gaillard, & Camos, 2009; Cowan et al., 2003; Hitch, Towse, & Hutton, 2001; Towse, Hitch, & Hutton, 1998). Some have suggested that developmental improvements in the amount of information that can be held in working memory stem from the development of mnemonic strategies, for instance “chunking” (e.g., Chi, 1976; Dempster, 1978). However, this seems unlikely in the visuo-spatial domain, since the advances are largely linear across development. Others have suggested that developmental improvements in performance stem from increased capacity, or “storage space”, per se (Pascual Leone, 1970). Others have argued that developmental improvements stem from increased efficiency in performing the secondary

processing task, freeing up more resource for the storage task (e.g., Case et al., 1982; Cavanagh, 1972). One example of the latter account would be the time-based resource-sharing account (TBRS, e.g., see Barrouillet et al., 2009), according to which three principles determine load on a complex span task: (i) the amount of available ‘attention’; (ii) the rate of decay; and (iii) the efficiency with which memory items can be reactivated when ‘attention’ is applied. The same flexible resource or ‘attention’ can be applied to either the maintenance of items, or to the processing required by the secondary task. When participants attempt to maintain items, their attention has to be re-allocated from that maintenance process, to the secondary processing task, and then back again before the memory items are lost to decay. This generates an interesting prediction: developmental increases in performance ought to be underpinned by an increased ability to use short pauses in the secondary task to reactivate memory items, rather than an increase in ‘capacity’ per se. Even when controlling for baseline differences in children’s ability (the time taken) to perform the secondary task, this was the case. The older the child (from 8 to 14 years), the greater the effect of the rate of the secondary task on their memory performance was. The authors argue that younger children are overly distracted by the processing task and are unable to switch their ‘attention’ back to the maintenance task. Whilst much remains unclear about how the TBRS account fits in with the existing literature (e.g., for example, what is meant by ‘processing resources’ and ‘attention’), it generated and tested developmental predictions on what drives developmental improvements in verbal working memory capacity, although alternative accounts have also been put forward that do not require resource sharing (e.g., Towse et al., 1998).

There is far less research exploring the reasons underlying developmental increases in capacity in the visuo-spatial domain (e.g., see Hitch et al., 1988; Hitch, Woodin, & Baker, 1989b; and Pickering, 2001 for a comprehensive review). It is unlikely that overlapping mechanisms limit both verbal and visuo-spatial short-term and working memory, since the mechanisms of visuo-spatial maintenance appear to be relatively unaffected by the suppression of verbal rehearsal (Morey & Cowan, 2004). However, we can conceive of (at least) three possible alternative explanations of why VSTM capacity increases with development: (i) many theorists have advocated a slots account explanation of VSTM capacity limits in adults (e.g., Zhang & Luck, 2008), and accordingly we might expect developmental increases in this capacity limit to stem from an increase in the number of available slots; (ii) some have advocated a flexible resource account of VSTM capacity limits in adults (e.g., Bays & Husain, 2008), in which case developmental increases could stem from an increase in the amount of this resource, or an increase in the extent to which it can be flexibly applied to either the precision or capacity of VSTM items; and (iii) some have argued that VSTM capacity limits in adults are largely determined by the extent to which they can use attention to gate what gains access to that storage (e.g., Fukuda & Vogel, 2009) and, based on this account, developmental increases would largely stem from an increasing ability to filter sensory input. The measures required to distinguish these various accounts are particularly sophisticated, and require the researcher to measure not only the extent to which an item is successfully maintained in VSTM, but also the precision with which it is maintained. Sadly, to our knowledge, no one has analysed developmental data on VSTM to contrast slot-based vs. precision accounts; this is certainly something that needs doing in the future. Some progress, however, has been made in assessing the extent to which the development of VSTM might be underpinned by developmental increases in attentional filtering abilities (i.e., the efficiency with which information is encoded and attentional capture by irrelevant materials resisted); much of the work of Cowan and colleagues has focussed on this question.

Cowan, Morey, AuBuchon, Zwilling, and Gilchrist (2010) presented children with arrays of two types of shape (circles or triangles) of in various colours, and after a delay one of those shapes re-appeared as a memory probe at that same location either in the same of in a different colour (with a variety of colour changes, including trials in which the colour was entirely novel for that trial, and trials in which the changed-to colour was that of an old shape presented at a different location in the memory array). On a block-wise basis they varied the probability of any shape type returning as the probe. On some blocks only one shape type was presented, meaning that no filtering on the basis of shape was possible. These trials provided a baseline assessment of capacity. On some blocks, at encoding shapes were mixed, but one shape type always appeared as the probe – making attending to objects of that shape (i.e., filtering the others out) an advantageous strategy on every trial. On some blocks one shape-type was 80% likely to re-appear as the probe, and the other shape-type only 20% likely to re-appear as the probe—making filtering an advantageous strategy, although one that should results in costs in the infrequent trials in which the unattended shapes re-appeared as probes. Finally, on some blocks either shape was equally likely to re-appear as the probe and participants were explicitly asked to attend to both. By comparing the extent to which performance was modified by the different filtering conditions, Cowan and colleagues were able to examine the extent to which children aged either 7–8 or 12–13 and adults were able to bias their storage strategically. At a load of 2 items, despite the youngest children being much worse than the other two groups, the profile of performance across the conditions was very similar. However, at a load of 3, it became apparent that the two older groups were significantly better at biasing their storage—favouring those items most likely to re-appear in the memory test. It makes good sense that only when storage is stretched, for instance by increasing load, that it becomes necessary to use filtering to maximise the capacity available (or to exclude irrelevant items from consuming that capacity).

A further piece of the “attentional puzzle” in the context of developmental changes in VSTM comes from another elegant study by Cowan and colleagues: Cowan, Naveh-Benjamin et al. (2006) asked whether the ability to maintain information about the binding between an object and its spatial location changes with development across the life span more than memory for simpler item (its colour) information. Consonant with the change-detection paradigms reviewed above, paired arrays of coloured squares were presented to participants and were either identical or differed in the colour of one square. A circle surrounding one square in the second, test array indicates which square changed colour, if any square did, and the required response was a judgment as to whether a colour change occurred. In the latter case, the changed colour was unique on that trial (item colour change) or, in a more attentionally demanding condition, was duplicated elsewhere in the array (requiring participants to notice that an already-present colour was now also present at the cued and new location). Performance levels in young adults should be excellent with up to about four squares per array and quickly drop as a function of array set sizes beyond four, but previous findings (Wheeler & Treisman, 2002), predicted that focused attention would be required to a greater degree to create and maintain binding information over time. When binding and item changes were presented in separate blocks, both children (8–10 and 11–12 years old) and older adults (65–85 years old) showed differentially greater deficits relative to young adults in detecting accurately binding compared to single item changes, with an additional deficit in older adults when item and binding trials were intermixed and their increasing tendency to report no change for binding trials across blocked and mixed conditions. The findings indicated inverted-U shape changes in the ability to maintain information in memory, especially when binding is required,

accompanied by bias-related processes that influence the use of binding information monotonically. Furthermore, the children’s decrements in performance when binding was required were also replicated by larger developmental differences when children were required to bind colour and location by Cowan et al. (2010). Finally, when Cowan, Elliott et al. (2006) asked young adults to divide their attention between the same visual change detection conditions and concurrent (and irrelevant) auditory judgments sensitivity to changes deteriorated across conditions, pointing to the role of focused attention in maintaining and recalling information from VSTM across conditions. More broadly, this study also underscored the useful role of life-time developmental trajectories in pinpointing distinct parameters leading to developmental changes in VSTM capacity.

Of course, attentional control abilities cannot explain all of these developmental improvements in capacity. For example, in Cowan et al.’s (2010) data, even on trials that did not require filtering per se, the youngest children were far worse than the other two groups, yielding K estimates of approximately 1.5, indicating very basic and reliable storage differences across age groups even under these conditions. Intriguingly others (e.g., Riggs et al., 2006) found higher estimates of K in a similar age group assessed with a simpler change detection task, suggesting that these storage limits are, at least to some extent, dependent on task demands. Nonetheless, Cowan and colleagues’ data demonstrate that it is especially when memory load is high, or when attentionally-demanding binding of colour and location information is required, that developmental differences are apparent. In short, attentional improvements provide some account for developmental improvements in capacity, but they certainly cannot be the whole story.

Our view is that developmental improvements in short-term and working memory in the visuo-spatial domain are likely driven by a number of factors and these need not be the same factors that produce individual differences, per se. For instance, in the data of Cowan et al. (2010) substantial improvements arise with development that cannot be explain purely by improved filtering. That said, we should be aware that overcoming the adverse effects of infrequent to-be-ignored items whose salience is manipulated over the duration of a block may be a rather gross measure of the precise mechanisms of attentional filtering deployed on a trial-by-trial basis. For example, different individuals and age groups may differ in the ability to deal with infrequent items because they do not process them well at the encoding stage (and so, paradoxically, incurring in relatively smaller costs when they surreptitiously re-appear), or because they are poor at recovering from their salient re-appearance at the recall stage (resulting in poor recall even if they had been equally capable of ignoring them). As these two types of effects would actually cancel each other out, even equivalent performance below capacity limits could be driven by different costs and benefits across attentional filtering conditions. In addition and beyond the findings above, there are some very obvious cases in which attention may be required to maximise VSTM capacity: poor attentional control could result in the intrusion of to-be-ignored items in the opposite hemifield (Vogel et al., 2005), or, in a more applied setting, interference from auditory distracters in a noisy classroom (akin to the conditions that adversely affected young adults’ performance in Cowan, Elliott et al., 2006; Cowan, Fristoe et al., 2006; Cowan, Naveh-Benjamin et al., 2006; Cowan, Sauls et al., 2006), or even by previously seen pieces of information that were not explicitly linked to the task at hand but were nonetheless stored in long-term memory (e.g., Chun & Jian, 1998, in adults and Dixon, Zelazo, & De Rosa, 2010, in a developmental context). In addition, the result of developmental changes in attentional control could be much more subtle and context-driven because, when remembering various items simultaneously, previously presented items are likely to interfere with one another, and perhaps to a

greater detriment in children—in some sense, even when no ‘distracters’ per se are present, the confusability of items is possible and may be dependent on both how well established and differentiated representations for the target items are, as well as how efficient resistance to interference from the target set may be. In other words, attention may play a critical role in the encoding of individual items/objects and their spatial locations using relatively distinct neural codes, to prevent the items from interfering with one another.

In sum, whilst there is good evidence that individual differences in VSTM in adults and visuo-spatial working memory capacity in children are constrained by attentional filtering, its involvement in determining developmental increases in capacity is far from clear. In the future, developmentalists could be informed by the adult cognitive literature, which has produced some elegant means of exploring potentially different limits of visuo-spatial storage (Bays & Husain, 2008; Zhang & Luck, 2008). What seems clear so far is that attentional filtering alone cannot explain developmental increases in VSTM capacity. A further fruitful approach for the future would be to look at attentional filtering in tasks that do not have an explicit storage requirement (as for example the attentional blink paradigm used by Fukuda & Vogel, 2009) and relate performance on these to developmental differences in VSTM and VWM, both measured through traditional span tasks and with K. Last, but not least, a longitudinal approach could investigate whether, and if so, how early attentional filtering abilities constrain later measures of span.

4. Insights from the developmental cognitive neuroscience of visual working memory

Some headway in understanding how attentional control and visual working memory relate over developmental time has been gained from investigating the development of neural circuits underlying both sets of processes. A series of studies in adults have demonstrated that VSTM tasks, requiring the maintenance of series of spatial locations, recruit a broad network of areas, typically including the intra-parietal sulcus and the dorsolateral prefrontal cortex (e.g., Cabeza & Nyberg, 2000; Curtis & D’Esposito, 2003; Funahashi, Bruce, & Goldman-Rakic, 1989; Naghavi & Nyberg, 2005; Sakai, Rowe, & Passingham, 2002; Todd & Marois, 2004; Xu & Chun, 2006). Multiple studies have also now demonstrated that activity in these areas increases with age when participants are asked to maintain information in VSTM (e.g., Klingberg, Forssberg, & Westerberg, 2002; Kwon, Reiss, & Menon, 2002; Thomas et al., 1999; Thomason et al., 2009). For example, Thomason et al. (2009) used a simple task requiring the maintenance of spatial or verbal information of increasing load over three seconds, before being asked whether a probe location or letter matched the initial display. Whilst children recruited similar areas of frontal and parietal cortex to adults in performing the task, adults exhibited greater activation in large regions of the frontal, parietal, and temporal lobes, basal ganglia, and cerebellum during the task. In addition, in children the activity in those areas did not increase with increasing load to the same extent as in adults. Thomas et al. (1999) assessed visual working memory across age groups and showed a broader right-lateralised network including the right superior frontal gyrus, right DLPFC, right superior parietal lobule—again across both children and adults. The more diffuse areas of activity in the latter study, by comparison with other groups (e.g., Klingberg et al., 2002), may stem from important differences in the VWM task used. Klingberg and colleagues used a task requiring the maintenance of visual items without their concurrent manipulation or processing (i.e., VSTM, according to our definition), whereas Thomas et al. used an n-back task that required substantial online processing in addition to storage (i.e., a VWM task). These commonalities but also differences in patterns of activations and in

age-related differences associated with them for distinct VSTM and VWM tasks support our excitement for convergence in the field, but also our earlier (cognitively defined) note of caution in comparing across these tasks.

Neural evidence also supports some of the classical distinctions in the cognitive developmental literature on working memory. There is increasing evidence that this fronto-parietal network is largely right-lateralised for visuo-spatial working memory, and that there is a left-lateralised network associated with verbal short-term memory. Thomason et al. (2009) contrasted the activity associated with VSTM maintenance with those areas in verbal maintenance, demonstrating large differences across the two domains. Again using an n-back task, Kwon et al. (2002) demonstrated that this right-lateralised fronto-parietal network shows protracted development that continues into early adulthood. A reasonable hypothesis, then, is that the improved functioning of this network over developmental time results in gradual increases in VSTM. Whether or not one uses a simpler VSTM task, or a more complex visuo-spatial working memory task, will likely influence the extent of frontal involvement, but a fronto-parietal network involvement appears to be common to both. As a word of caution, it is necessarily difficult to interpret neural differences revealed by neuroimaging studies of VSTM between children in adults. A well accepted approach is to design the task such that performance in children and adults can be equated in terms of accuracy, implying that any functional differences observed cannot stem from the generic difficulty of the task, but rather from the differential recruitment of task-related areas across the age span, but this is also fraught with problems: specifically in the context of n-back tasks, for example, this type of design may require comparing conditions (e.g., 0-back in children and 1- or 2-back in adults) that differ radically and perhaps non-monotonically in terms of their maintenance requirements (e.g., see Church, Petersen, & Schlaggar, 2010, for a discussion of this and other issues).

Olesen, Nagy, Westerberg, and Klingberg (2003) also explored the development of this fronto-parietal VSTM/VWM network in a cross-sectional design. They assessed a sample of 8–18 year olds performing a dot-matrix VSTM task. In addition to examining functional changes they also examined structural changes across developmental time. They used diffusion tensor imaging, taking fractional anisotropy (FA) as a proxy of white matter microstructure, alongside more conventional functional MRI. They observed a significant positive relationship between FA values and local grey matter activation levels within the superior frontal sulcus and inferior parietal lobe, areas that could form a functional network underlying VSTM/VWM function. Interestingly, with regard to relationships between structure, function and development, of course, that both grey and white matter correlate in their changes over time does not elucidate the causal factor in this relationship. For instance, it could be that increases in myelination or axon thickness result in the increased activity in the surrounded grey-matter, in turn driving increased neural activity and BOLD signal. By contrast, it could be that white matter changes are induced by the increased activity of these regions. Indeed, it is not necessarily clear whether we would predict an increase in neural activity over time, or a reduction over time, as neural circuits become more refined (see Brown, Petersen, & Schlaggar, 2006; Dick, Leech, Moses, & Saccuman, 2006; Durston & Casey, 2006; Durston et al., 2006). Nonetheless, all findings above pinpoint distributed right fronto-parietal involvement in visual short-term and working memory. With connectivity studies, growing targets for investigation have been not simply individual nodes in this network, but also how they operate in ensemble, and perhaps differentially so over developmental time. For example, in a study investigating neural activity at rest, Fair et al. (2007) tracked changes in inter and intra-network connectivity using spontaneous

synchronisation and desynchronisation in fMRI in fronto-parietal networks similar to those mentioned already. In adults there were (at least) two relatively distinct networks – the fronto-parietal and cingulo-opercular networks. These subserved subtly different control functions in adulthood. In childhood, however, there seems to be a much lesser degree of intra-network connectivity for instance between the intraparietal sulcus and superior prefrontal cortex. By contrast, children show a greater degree of connectivity between the frontal areas that are parts of separate loops in adulthood, for instance between anterior pre-frontal cortex and dorsolateral prefrontal cortex. It would seem that, as children develop, they undergo a gradual process of modularisation of neural networks. Thus, developmental increases or decreases in activity per se might not be particularly informative; rather this increasing functional specificity/segregation might drive the developmental changes we see in performance (as suggested by Scherf, Sweeney, & Luna, 2006).

These questions of the relationship between neural structure, function, development and capacity aside, it is directly pertinent to the focus of the current review to consider what exactly this network is doing such that its development may be related to improvements in VSTM performance. Interestingly (particularly in light of this review and special issue topic), these areas are also typically recruited during tasks requiring top-down attention control, but not explicitly storage (e.g., Hopfinger, Buonocore, & Mangun, 2000; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999) and overlap in the networks recruited for these have been compared directly in adults (LaBar, Gitelman, Parrish, & Mesulam, 1999). In an oft-cited developmental example, Adelman et al. (2002) used the Stroop task to chart the development of neural mechanisms of top-down control. They observed that areas in the parietal cortex recruited by this task are very similar in adolescents and adults, whereas prefrontal regions that are also recruited in VSTM tasks, show a much more protracted development. The best example of a developmental study that explicitly relates neural mechanisms of top-down attention control and VSTM comes from Olesen, Macoveanu, Tegner, and Klingberg (2007), who tested both of these functions in a combined design. They presented a group of young adolescents (aged 13) and a group of young adults with a set of to-be-remembered dots. Once these had disappeared, and after a maintenance delay, participants were presented with a line, and had to indicate the location on the line at which the location of a previously presented dot had been. Overall, adults were far more accurate at this task, implying that they had maintained a more precise representation of the dots across the memory delay. Mirroring this behavioural effect, adults showed increased activation in “the usual suspect”, the fronto-parietal network – specifically superior frontal sulcus and intraparietal sulcus – relative to children. On some trials, during the maintenance period, Olesen et al. (2007) also presented a set of distracter dots. Despite the fact that these were to-be-ignored, performance on distracter trials was worse than on standard trials and performance was impaired to a greater extent by distracters in the group of adolescents relative to adults. Mirroring this interaction between age and distraction, the superior frontal sulcus showed greater activity in adolescents, relative to adults, on distracter trials. The implication is that those areas recruited for storing to-be-remembered items are also recruited by children for to-be-ignored items. Whether this different neural response to distracters in adolescents and adults indexes ineffective distracter suppression mechanisms (i.e., attentional filtering difficulties, as proposed by Vogel and colleagues for differences between adults of high and low VSTM capacity, e.g., Fukuda & Vogel, 2009) or inappropriate recruitment of storage mechanisms under conditions of distraction on the part of the adolescents remains unclear. However, the findings do highlight the fact that developmental changes in capacity are mirrored not just by developmental changes in the neural response to to-be-stored

items, but also by changes in the neural response to to-be-ignored items.

More broadly, all studies reviewed in this section point to a great degree of overlap in the neural networks involved in VSTM/VM and attentional control and recent attempts to study how the interplay of attentional and VSTM processes operate over developmental time. In turn, therefore, they underscore a role for developmental cognitive neuroscience in bridging between two disciplines that, thus far, have tended to operate in isolation.

5. Insights from training working memory

As has previously been mentioned, there are large individual differences in both VSTM and visuo-spatial working memory across children. In recent years there has been a great deal of interest in the extent to which low working memory capacity can be boosted with training in preschoolers, school-aged children and adults (see Klingberg, 2010, for a recent and comprehensive review). For example, Klingberg et al. (2005) demonstrated that in a group of 53 children with ADHD aged between 7 and 12 years of age, substantial improvements in working memory could be achieved by adaptive training. Children showed significant increases in multiple outcome measures – in VSTM, verbal working memory, response inhibition and complex reasoning – when the training difficulty increased incrementally relative to when it did not. More recently, improvements have also been demonstrated in a group selected on the basis of low working memory (rather than meeting clinical diagnostic criteria for ADHD per se) that substantial improvements in visuo-spatial and verbal short-term and working memory can arise from this adaptive training (Holmes, Gathercole, & Dunning, 2009). The benefits transfer to novel tasks, are maintained across relatively long time spans (at least 6 months), and can result in improvements on a measure of academic achievement (e.g., mathematics). Furthermore, these training benefits have also been replicated in preschoolers (Thorell, Lindqvist, Nutley, Bohlin, & Klingberg, 2009), suggesting that training programs and their outcomes may be successfully studied from early childhood. Moreover, neuroimaging data have revealed that these training benefits are mirrored by increased activity in the parietal and frontal regions recruited in VSTM tasks (e.g., Olesen, Westerberg, & Klingberg, 2004).

As academics we search arduously to identify individuals with limited memory capacity amongst our well educated university student populations, in order to conduct meaningful studies of individual differences in capacity. (That it is difficult to find individuals with poor working memory in a university setting ought to tell us something.) Educationalists and developmentalists researching within the state education system, by contrast, are regularly confronted by the consequences of low short-term and working memory capacity. The growing finding from the developmental literature is that short-term and working memory capacity is malleable and not entirely genetically predetermined, but at least partly determined by environmental experience such as training (Klingberg, 2010). One distinct possibility is that this training results in changes in attentional control, rather than in extending capacity per se. These enhanced top-down control mechanisms may enable children who have undergone training to control better what gains access to storage, and thus to maximise their available capacity. Future work will be needed to address the question. Nonetheless, adult VSTM and working memory theorists should look on with great interest – for instance, does working memory training produce better attentional filtering (Vogel and Fukuda, 2009), an increased number of slots available (Zhang & Luck, 2008), or an increased amount of flexible resource (Bays & Husain, 2009)? By contrast, would direct training in attentional control (e.g., as in Rueda, Rothbart, McCandliss, Saccomanno, & Posner, 2005; Tang & Posner, 2009) transfer to increases in VSTM capacity?

6. Conclusions

We began by asking whether five overlapping questions about the nature of VSTM and VWM capacity limits could be addressed by investigating their developmental origins and individual differences. An obvious but important point is that the extent to which visual attention might be critical to any visual working memory task is likely to vary massively depending upon the task used. First, we therefore asked whether measures used to tap VSTM and VWM in the developmental and adult literature are commensurate with each other. In drawing comparisons between the developmental and adult cognitive neuroscience literature, we were particularly struck by the discrepancy between the measures typically used, and the differences in the constructs that they are thought to tap. Despite these, we found growing evidence that the developmental and adult literatures can inform one another. Our second line of enquiry focused, for instance, on the role played by individual differences in attentional control in accounting for VSTM and VWM capacity. Like in the adult VSTM literature, a significant proportion of the individual differences in children's performance on spatial working-memory tasks can be predicted by their attentional filtering abilities. Our third question, however, explored whether developmental changes in capacity (rather than individual differences at each point in development) could be driven by changes in attentional control. In this context, the relationship between attention and VSTM/VWM increases over development is as yet unclear. The work of Cowan and colleagues demonstrates that developmental increases in capacity cannot be purely explained by improved attentional filtering and certainly need to be further investigated. As a fourth set of illuminating findings, we turned to the growing literature exploring the neural substrate of developing VSTM capacities, but relatively little work has explored the exact functional significance of developmental changes in frontoparietal activity for developmental increases in capacity. Top-down attentional control is strong candidate for the role of this network, though this hypothesis has yet to be fully investigated. Studies by Klingberg and colleagues suggest that developmental changes in VSTM capacity are mirrored not just by developmental changes in the neural responses of to-be-stored items, but also by changes in the neural responses of to-be-ignored items, i.e., in the efficiency with which the latter are suppressed and/or do not inappropriately recruit storage mechanisms. A fifth and thriving field of developmental research has begun to question the extent to which VSTM and VWM are inflexible because controlled and targeted environmental interventions, in the form of WM training, seem to have lasting effects on capacity in both children and adults. The precise mechanisms for these changes remain unclear. In conclusion, then, distinct sources of evidence converge on suggestion that improvements in how attentional biases operate to enhance task-relevant and suppress task-irrelevant dimensions of sensory input are a likely and testable target for the developmental and adult cognitive neuroscience of VSTM and VWM.

Q3 Uncited reference

Fukuda and Vogel (2010).

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