Executive functions and self-control

William von Hippel

University of Queensland

Richard Ronay

University of New South Wales

This research was supported by grants from the Australian Research Council. Address Correspondence to William von Hippel, School of Psychology, University of Queensland, St Lucia, QLD 4072 Australia, billvh@psy.uq.edu.au

Despite unimpressive tooth and claw, in little more than 100,000 years humans have worked their way to the top of the food chain. This success is due in large part to the evolution of large frontal lobes that allow humans to negotiate complex and highly effective social relationships (Dunbar, 2007). One important suite of abilities located in the frontal lobes are the executive functions, which are responsible for planning, coordinating, and integrating the basic cognitive and affective processes with which people navigate their everyday existence. A critical component of executive functioning is the ability to *inhibit* inappropriate thought and action (Dempster, 1992; Hasher & Zacks, 1988; Hasher et al., 1999). Inhibition is necessary for negotiation (and subsequent compromise) of competing goals, and also for the delay of gratification required to pursue long-term goals once they are chosen (Dunbar, 1992; Eigsti et al., 2006). These important tasks place inhibitory ability at the center of successful social functioning.

It is easy to imagine how inhibitory control might have evolved in humans, as increasingly complex social interaction would have placed a premium on voluntary control over appetitive and aggressive urges (Bjorklund & Harnishfeger, 1995). Thus, the evolution of self-control probably began with the development of the prefrontal cortex and its connections with the limbic system. According to this view, inhibition is likely to be integral to social harmony, as it allows people to withhold strong responses while considering the personal, social, and long-term implications of their actions. In this chapter we explore the relationship between executive functioning and self-control by examining two types of self-control failure. The first type of self-control failure we consider is that brought about by age-related declines in inhibitory functioning. Here we review research on the

manner in which age-related losses in executive control can lead to increased prejudice and social inappropriateness, and under certain circumstances, increased depression and problem gambling. The second type of self-control failure we consider is that brought about by the availability of mating opportunities. Here we review research on the manner in which mating opportunities lead to increased risk taking and the possible role of executive functions in this effect.

AGING, INHIBITION, AND SELF-CONTROL

In late adulthood the brain gradually shrinks in total volume and weight. The frontal lobes in particular show atrophy with age (Dempster, 1992). Because the frontal lobes are the seat of executive functions, including tasks such as planning and controlling thought and behavior (Banfield et al, 2004; West, 1996), an important consequence of atrophy of the frontal lobes is poor executive functioning, including reduced ability to inhibit irrelevant or unwanted thoughts (Dempster, 1992; West, 1996). Because such failures at thought control lead to contamination of ongoing mental activities with unwanted information, age-related deficits in inhibitory ability have been implicated in a variety of cognitive deficits (Hasher & Zacks, 1988; Hasher et al., 1999). Inhibitory processes are also theoretically linked to a variety of social phenomena, but to date there are only a few empirical investigations of the impact of age-related inhibitory losses on social functioning.

Aging, inhibition, and prejudice: Older Americans tend to be more prejudiced than their younger counterparts (Schuman et al., 1997; Wilson, 1996). This age difference is thought to be related to the historical periods in which the different generations were socialized, and indeed people were more prejudiced 30 and 50 years ago than they are today (Schuman et al., 1997). Nevertheless, this “generational” explanation for age differences

in prejudice might be only part of the story, as older adults might have greater difficulty than younger adults inhibiting unintentionally activated stereotypes.

In an influential model of prejudice, Devine (1989) proposed that because our culture is suffused with stereotypes concerning African-Americans, these stereotypes become over-learned and are automatically activated upon encounters with individual African-Americans. What differentiates non-prejudiced from prejudiced individuals in this model is not whether prejudiced thoughts are activated, but whether individuals inhibit those thoughts and replace them with more egalitarian beliefs. Prejudiced individuals are thought to endorse the stereotypic thoughts that are automatically activated, and non-prejudiced individuals are thought to reject and subsequently inhibit the stereotypic thoughts. Thus, an important implication of this model of prejudice is that individual differences in inhibitory ability should be associated with individual differences in prejudice. Because older adults have greater difficulty inhibiting unwanted information (Hasher & Zacks, 1988; Hasher et al., 1999), this model of prejudice suggests that they might become more prejudiced than younger adults due to their more frequent failure at inhibiting their stereotypes.

Consistent with this line of reasoning, we found that older white adults show greater stereotyping and prejudice toward African Americans than younger white adults, despite being *more* concerned about impression management and *more* motivated to control their prejudices (von Hippel, Silver, & Lynch, 2000). Furthermore, when we measured inhibitory ability (by giving participants paragraphs that contain distracting text and asking them to read the paragraphs aloud without vocalizing the distracting text; see Connelly et al., 1991), we found that the age differences in stereotyping and prejudice were mediated

by age differences in inhibition. That is, older adults only showed greater stereotyping and prejudice to the degree that they also showed greater difficulty inhibiting their vocalization of the distracting text. Additionally, individual differences in inhibition were associated with individual differences in prejudice among both older and younger adults, suggesting that the inhibition/prejudice link in older adults is not simply a byproduct of incipient dementia.

Three types of studies have now provided results that extend these earlier findings. First, Radvansky, Copeland, and von Hippel (2008) conducted an experiment in which older and younger adults were presented with stories that contained stereotypic content that was hinted at, but not stated explicitly. After such inference-inviting sentences, participants were occasionally interrupted to complete a lexical decision task assessing activation of a word highly related to the inference (e.g., after the sentence, "*Susan saw that Jamal didn't help*", participants were tested with the word *lazy*). Participants were also tested after inference-inviting sentences that were stereotype neutral and after sentences in which no inference was likely (used as control sentences). Results revealed that compared to the control sentences, younger adults were faster to identify the inference-relevant neutral words, but slower to identify the inference-relevant stereotypic words. In contrast, older adults were also faster to identify the inference-relevant neutral words, and non-significantly faster to identify the inference-relevant stereotypic words. These findings suggest that younger adults are inhibiting their stereotypic inferences on-line, but older adults are failing to do so.

Second, Gonsalkorale, Sherman, and their colleagues (2007) conducted secondary analyses of web-based IAT data that were collected with very large samples. Their analy-

ses relied on the Quad Model (Conrey et al, 200x) to parse people's IAT scores into four different subcomponents. For our purposes, the most important subcomponent is what they call *overcoming bias*. This measure indicates people's ability to over-ride any bias they might have toward the target category. In their secondary analyses, Gonsalkorale et al. (2007) find that older adults show greater prejudice than younger adults on the IAT because they have greater difficulty overcoming bias.

Third, in a very different type of paradigm, Henry, von Hippel, and Baynes (2007) conducted a study in which older adults' peers reported on a variety of their behaviors. One aspect of their behavior that was included in the peer report was the tendency to rely on stereotypes and to be prejudiced toward others based on race or ethnicity. Henry et al. found that participants' peer reports of their tendency to rely on stereotypes and to be prejudicial were predicted by the participants' own scores on measures of inhibitory functioning (measured via the Trail Making Test). Furthermore, the predictive ability of the inhibitory measure was independent of the participants' scores on a measure of cognitive functioning designed to assess incipient dementia and was also independent of a measure of perspective taking. These findings suggest that inhibition plays an independent role in increased prejudice with age, beyond that which might be caused by diminished cognitive functioning in general, and beyond that which might be caused by age-related deficits in theory of mind.

These data suggest that because prejudice toward African Americans conflicts with universally held egalitarian beliefs, older adults attempt (but fail) to inhibit their racist feelings. Not all prejudices conflict with egalitarianism (Crandall & Eshleman, 2003), however, and thus not all age differences in prejudice should be mediated by inhibitory

deficits. For example, people who are prejudiced against gays perceive homosexuality as a chosen lifestyle (Herek, 1994), and thus for them anti-gay prejudice does not conflict with egalitarianism (and thus is unlikely to be met with inhibitory efforts). These attitudes themselves are highly correlated with social conservatism and fundamentalist religious beliefs (Altemeyer, 2003; Herek, 1994), suggesting that age differences in anti-gay prejudice may have more to do with conservatism than with inhibitory failure. Consistent with this line of reasoning, a nationally representative survey of older and younger white Americans revealed greater prejudice toward gay men and African Americans among older than younger respondents. Importantly, the increased prejudice toward gay men among older adults was fully mediated by age differences in conservatism, whereas the increased racism among older adults was unrelated to conservatism (von Hippel, Radvansky, & Copeland, 2008). Thus, some age differences in prejudice (e.g., anti-gay prejudice) might represent cohort effects whereas others (e.g., anti-Black prejudice) might not.

Aging, inhibition, and social inappropriateness: Age-related inhibitory losses have also been implicated in two other types of social inappropriateness. First, older adults are more likely than younger adults to talk excessively and about topics that are irrelevant to the stream of conversation (Pushkar et al., 2000). This increase in "off-target verbosity" is associated with diminished inhibitory ability (measured via the Trail Making Test, the Stroop test, and verbal fluency), which leaves older adults less capable of stopping their conversation and remaining on topic.

Inhibition might also be necessary to restrain ourselves from verbalizing thoughts that are better left unsaid, and thus inhibitory deficits might lead older adults to make socially inappropriate remarks. Consistent with this possibility, we found that older adults were

more likely than younger adults to inquire about private issues in public settings (e.g., about family problems or possible weight gain), and this age difference in social inappropriateness was mediated by inhibitory deficits (von Hippel & Dunlop, 2005). In this study, inhibition was measured with a trivia test that includes bogus items that require respondents to inhibit their prepotent response (e.g., responding "Black", to, "What color are a tiger's spots?"). Furthermore, these age differences emerged despite the fact that older and younger adults agree that it is inappropriate to inquire about such issues in public settings (and indeed older adults in particular felt less close to those who inquired about private issues in public). These findings suggest a dissociation between knowledge of social rules and the ability to follow them that is consistent with other types of frontal lobe damage (reference).

These findings have now been replicated and extended in the study mentioned above, in which peers reported on older participants' behavior outside the lab (Henry et al., 2007). Along with measures of prejudice, participants' peers also reported on their socially inappropriate behavior (e.g., "embarrasses people unintentionally"). As with the prejudice measure, peer-rated social inappropriateness was related to inhibitory ability (as measured by the Trail Making Test), independent of scores on a test of general cognitive functioning and independent of scores on a perspective taking scale.

These studies have the advantage that they link the report of participants' peers to their own inhibitory functioning, but they have the disadvantage that the behavior of interest is taking place outside the lab, and thus in a manner that is unobservable. We have, however, made a few tentative steps in the direction of assessing social inappropriateness in the lab. First, in the Henry et al (2007) study we also gave them an opportunity to say

something inappropriate by “inadvertently” having a screen saver emerge on the computer screen in which the young Caucasian female experimenter is depicted in a love-heart with an older Aboriginal male. When older and younger adults then evaluated the expressions and comments recorded by a hidden camera, their ratings of the inappropriateness of participants’ responses to the screen saver were predicted by the peer reports of social inappropriateness outside the lab. Additionally, ratings of the inappropriateness of participants’ responses to the screen saver were also predicted by a measure of inhibitory functioning (the fluency test). However, fluency scores did not significantly predict peer-reported inappropriateness, and they only predicted responses to the screen saver among participants who showed no signs of dementia on the cognitive screening measure. Thus, these results must be considered tentative at this point in time.

In a second effort to assess social inappropriateness in real time we conducted a study in which we manipulated inhibitory ability in an effort to see if it would lead to changes in social inappropriateness. To manipulate inhibitory ability, we relied on the fact that circadian rhythms are known to influence inhibitory ability, with older adults typically showing better inhibition earlier rather than later in the day and younger adults showing the opposite pattern (Hasher et al., 1999). These patterns of inhibitory functioning appear to reflect age-differences in broader circadian rhythms in biological and cognitive functioning that also emerge in non-human animals (Winocur & Hasher, 2004). In this study, older and younger Caucasian Australians were brought to the laboratory in the morning or late afternoon and told that we were interested in their opinion on international events. Ostensibly to provide them with an example of the type of opinion we were interested in, the Chinese experimenter provided an example of his own opinion that was designed to

provoke an argument (i.e., he noted that he thought China would soon be the world's superpower). Participants were only told this information in passing, and were not asked to comment on it, and thus any arguments with the experimenter at this point can be considered gratuitous. Both young and old adults were highly unlikely to argue with the provocateur in the morning, but almost half of the older participants spontaneously voiced their disagreement when tested in the afternoon. These results suggest that deficits in inhibitory functioning led older adults to argue with the experimenter, but circadian rhythms influence cognitive functioning in a manner that is much broader than just executive control, so this finding awaits further research to assess the specific role of inhibitory functioning in the increased likelihood of engaging in gratuitous arguments.

These findings suggest that independent of other cognitive losses, older adults who show deficits in inhibitory functioning show related increases in their tendency to engage in socially inappropriate behavior. If these effects of inhibitory deficits really are distinct from the effects of incipient dementia, however, then it should also be the case that younger adults who have relatively poor inhibitory functioning are also more likely to make socially inappropriate comments. To test this possibility, von Hippel and Gonsalkorale (2005) told young adult Caucasian participants that they were participating in a study on the effects of food chemicals on memory. Half of the participants were then told by a Chinese experimenter that they were going to get to eat her favorite food, which was also the national dish of China. The other half of the participants were told by a Caucasian experimenter that they would be eating Chinese food. Independent of this manipulation, half of the participants were then asked to try to remember an 8-digit number, and half were not given this task. In close proximity to their face, the experimenter then

opened a dish containing an intact chicken foot, including the toenails, cooked in a Chinese style. A hidden video camera revealed that participants were least likely to make a negative expression or comment if they were not cognitively busy and if the Chinese experimenter had placed social pressure on them with her claims about the food's importance. Additionally, participants in only this condition also showed a relationship between their inhibitory ability (measured via the Stroop) and their tendency to make a positive or neutral expression or comment. These results with young adults suggest that increased social inappropriateness with age is not just a sign of early stages of dementia, as younger adults also appear to rely on their inhibitory skills to keep socially inappropriate thoughts in check.

Aging, inhibition, and depression: Poor inhibitory ability is not only associated with cognitive and social problems, it is also related to depression (Hertel, 1997). Although depression might cause inhibitory deficits, age-related inhibitory deficits might also contribute to late-onset depression by impairing control of excessive rumination (Davis & Nolen-Hoeksema, 2000). Note, however, that inhibitory deficits should not lead all, or even most, older adults to excessive rumination. Rather, only those older adults who rely on inhibitory control to stop themselves from ruminating (either chronically or when confronted by negative life events) are likely to develop problems with rumination if they have poor executive control. Older adults disinclined to ruminate and older adults who ruminate but do not try to suppress their ruminative thoughts should not show a relationship between inhibition and rumination.

Deficits in executive control are particularly apparent in depression having its initial onset in older adulthood (typically defined as at or after sixty years of age; for a re-

view see Alexopoulos, 2003). This suggests the possibility that inhibitory deficits may contribute to depressive symptoms because they bring decreased capacity for self-regulation in the face of negative life events. Additionally, age-related deficits in executive control may increase vulnerability to depression among older adults who may have been prone to depressogenic patterns of thinking throughout their lives. In sum, an inability to exert effective executive control over persistent negative or ruminative thoughts may contribute to depressive symptomatology in older adulthood. According to this hypothesis, late-onset depression is more likely to be associated with deficits in inhibitory function and executive control than is early-onset depression (for which poor inhibition is less likely to be a central causal factor). As such, among depressed older adults, late onset of symptoms should be associated with poor inhibitory ability, whereas early onset of symptoms may or may not be associated with inhibitory ability. Moreover, the relation between inhibitory deficits and late-onset depression should be mediated by rumination.

Consistent with this reasoning, we found that inhibitory deficits (measured via the Stroop test, the distracting text task described above, and a working memory task) predicted greater depression among late-onset but not early-onset depressed older adults, and that inhibitory deficits had their impact via their role in rumination (von Hippel, Vasey, Gonda, & Stern, in press). That is, among older adults with late-onset depression, poorer inhibition predicted increased rumination, which in turn predicted increased depression. In contrast, among older adults with early-onset depression inhibitory deficits were not associated with ruminative tendencies, suggesting that these individuals were not relying on inhibition to control their rumination, and in all likelihood had developed depression for other reasons.

In the case of depression, however, we cannot rule out the possibility that dementia is the root cause of the apparent relationship between inhibitory deficits and late-onset depression, as both are highly associated with dementia. Nevertheless, recent evidence suggests that inhibitory ability is also linked to rumination among younger adults (Whitmer & Banich, 2007), and thus further research might disentangle dementia from the relationship between inhibition and depression by focusing on a younger cohort. Although individual differences in executive control among younger adults are smaller than those among older adults, sufficiently sensitive measures might reveal that inhibitory functioning predicts depression across the lifespan in a subset of the population (those with ruminative tendencies that they control via thought suppression).

Aging, inhibition, and problem gambling: Analogous to the case with late-onset depression, poor inhibitory ability is unlikely to lead to gambling problems in all or even most older adults. Rather inhibitory deficits might lead to gambling problems only among those who struggle with their desire to gamble. That is, people who enjoy gambling might be at risk for developing gambling problems as they age, due to losses in the ability to restrain their urge to gamble. To test this possibility, we recruited older adults from various gambling establishments, and measured their level of gambling problems via a popular self-report measure (the South Oaks Gambling Screen, LeSieur & Blume, 1987). We found that older adults who gamble suffer from greater gambling problems to the degree that they also have poor executive control (measured via the Trail Making Test; von Hippel, Ng, et al., 2007). In a follow-up study, we replicated this relationship and also found that scores on the South Oaks Gambling Screen predicted greater geriatric depression via their impact on financial stress. Furthermore, these relationships emerged independent of

general cognitive functioning. These findings suggest that older adults who enjoy gambling develop greater gambling problems if they suffer losses in inhibitory control, and furthermore, that these gambling problems are important, as they appear to be causing significant levels of financial distress and consequent increases in depression.

The problem with these studies, however, is that they rely exclusively on self-report measures of gambling problems. If deficits in inhibitory functioning cause gambling problems among older adults because they make it difficult for them to suppress their urge to gamble, then they should lead to greater perseveration at gambling in the face of losses. In an initial test of this possibility, von Hippel and Hucker (2008) conducted an experiment in which older adults played a computerized gambling game with real winnings, either in the morning or the afternoon. The game was pre-programmed to appear random but initially provide more wins than losses. After participants had accumulated some winnings, they were told that they could continue to play for as long as they liked or until they lost all their winnings. Unbeknownst to them, at that point the program shifted so that the game no longer provided any wins, thereby enabling the assessment of perseverance in the absence of reward. Consistent with predictions, older adults responded more readily to the absence of reward and stopped playing more quickly in the morning than in the afternoon, and this effect was most pronounced among older adults whose circadian rhythms identified them clearly as “morning types”. These findings again implicate inhibitory deficits in gambling perseveration, but because circadian rhythms influence general cognitive functioning, beyond just inhibitory control, it remains for further research to establish that inhibition is the mechanism underlying this effect.

MATING, RISK-TAKING, AND SELF-CONTROL

Parental investment is a lopsided affair for humans and biological differences in reproductive capacity have led to the adaptation of different investment strategies across the two sexes (Trivers, 1972). For females, successful procreation comes at a considerable cost; gestation, birth, the nursing of infants and a greater role in the ongoing provision of care means that there is a reproductive ceiling for women that is not paralleled in males. If there is a ceiling for men, it is theoretically bound only by access to fertile mates and mortality. Under such circumstances, mate access becomes a reproductive resource attracting fierce competition (Dekel & Scotchmer, 1999), and sexual size dimorphism suggests a long history of polygamy amongst humans (Leigh, 1992), whereby males competed for access to females.

All forms of competition involve a level of risk, and in this case reproductive success rests upon an organism's responsiveness to the shifting scales of potential costs and benefits. In evolutionary terms, the fulcrum on which these scales rest is genetic survival, with the survival of any particular organism being important only insofar as it serves to meet this super-ordinate goal. Genetic replication is maximized via the selection of traits that ensure successful and prolific reproduction, and the greater the potential variation in reproductive success, the greater the competitive pressures of selection.

Both biologically and historically, the reproductive potential of males varies dramatically. One particularly intriguing line of evidence comes from the DNA study of Y-chromosomal lineage within Asia that finds eight percent of men within this region share

a common biological ancestor, who may well be Ghengis Khan (Zerjal et al., 2003). Genghis Khan was no stay-at-home, and it is hard to conceive of his more risk-averse contemporaries achieving such a legacy. The sedentary life might be less treacherous, and its appeals are not to be scoffed at – old age and a faithful family, while modest in comparison, are not a genetic cul-de-sac – but the pressures of selection mean that the spirit of the Khans endure in many men to this day. Thus, the tension between a desire for safety and survival and the allure of a more competitive, riskier path might be seen as an adaptive legacy that within a contemporary context, plays itself out in many maladaptive ways (Daly & Wilson, 2001, 2005; Wilson & Daly, 1985).

Inhibitory control is fundamental in maintaining this tension, providing a counterpoint to the more primitive limbic drives, such as the desire to mate (Bjorklund & Harnishfeger, 1995). Consider our proverbial anthropoid ancestor whose diminutive frame casts him as no match for the alpha male of his group. While he is sexually driven to mate, wantonly soliciting sex with the alpha male's harem would not end well. An inhibitory mechanism that served to temper such a drive might help him bide his time, strategize, and plan a more fruitful, albeit circuitous path to his goal and the subsequent survival of his genetic blueprint. Nevertheless, cues that signaled sexual invitation, an increase in one's immediate social power, or the opportunity to co-opt a particularly good combination of genetic material into one's own genetic legacy might be enough to shift the tension even in such an ancestor. In such cases, an adaptive response might be for self-regulatory "failure". Here we report on three preliminary studies that explore how the executive sys-

tems of young males respond to these contextual cues.

Physical Attraction, Risk-Taking and Self-Control

At a basic level, attractiveness signals an individual's genetic capacity to ward off environmental teratogens in utero, as well as other environmental assaults throughout development (Gangestad & Thornhill, 1994). Where female attractiveness denotes genetic fitness and therefore fertility, it also signals an increase in the potential gains associated with the kind of successful risk-taking that might lead to copulation and the possibility of reproduction. For this reason, a biological system that caused our ancestral male to focus on the here and now, to the exclusion of otherwise important considerations, in the presence of an attractive, potential mate, might have been adaptive.

One study that lends support to such speculation is Daly and Wilson's (2004) research documenting an increase in males' delay discounting after exposure to attractive female faces. Their finding suggests a type of inhibitory failure insofar as the decisions of participants in the attractive condition were more concerned with the present than those exposed to less attractive faces: The former opted for smaller immediate rewards, and the latter exercised some restraint by selecting the greater gains that lay in a less certain future.

To further test the possibility that the attractiveness of females might affect the self-control of males, we mirrored Daly and Wilson's (2004) manipulation and invited participants to view pictures of either highly attractive young women or a group of average attractiveness. All pictures were of faces alone, and in all photos the women's gaze was

directed towards the camera. In two separate studies, after viewing these faces and rating them for attractiveness and symmetry, males who viewed the attractive faces scored higher on the Thrill and Adventure Seeking subscale of the Sensation Seeking Scale (Zuckerman, 1994) and self-reported greater impulsivity.

Testosterone, Physical Attraction, Risk-Taking and Self-Control

One possible moderating influence on the relationship between physical attraction and self-control is testosterone. High testosterone males strive for positions of dominance, and short-term increases in testosterone help move high testosterone males toward positions of dominance, reducing fear, increasing assertiveness, violence, and competitiveness (Dabbs & Dabbs, 2000). In response to competitive cues, fluctuating testosterone levels might then contribute to reduced self-control and increased risk-taking. For males, one such cue might be exposure to females, and indeed such cues have been associated with short-term increases in testosterone (Roney, 2003) as well as the pursuit of short-term over long-term rewards (Daly & Wilson, 2004).

To bring these ideas together, we measured the 2nd to 4th digit ratios (2D:4D) of participants in our earlier studies as a marker of baseline testosterone levels (Manning et al., 1998) and greater sensitivity to testosterone (Manning et al., 2003), and found a positive relationship between 2D:4D and risk-taking behavior on a computerized risk-task, the Balloon Analogue Risk Task (Lejuez et al., 2002).[1] Importantly, this correlation held only

[1] The task presents people with the image of a balloon on a computer monitor, accompanied by a balloon pump operated via a mouse. With each pump, people accrue one cent in a temporary bank, however, with each additional pump they risk exploding the balloon and consequently losing all the money from their temporary bank. Participants can

for those who had viewed the attractive faces. In a follow-up study, participants completed the balloon task on two occasions, once after viewing the attractive faces and once after viewing the faces of average attractiveness. Higher levels of testosterone were predictive of relatively more risk-taking after viewing the attractive faces. Thus, the attractive females were causing enhanced risk-taking amongst those males whose digit ratios suggested higher levels of testosterone.

Testosterone, Physical Attraction and Executive Function

In an attempt to locate the inhibitory mechanisms by which these self-reported and behavioral expressions are altered, we began by measuring Stroop performance and working memory. Working memory was targeted due to its wide-ranging role in cognitive behaviours such as comprehension, reasoning and problem solving (Engle, 2002). More important to our purposes, neuroimaging studies have revealed working memory function to be particularly reliant on the dorsolateral pre-frontal cortex (DLPFC) and its role in blocking task-irrelevant information (Kane & Engle, 2002). We hypothesized that increases in risk-taking and impulsiveness might be concomitant with an inability to turn one's attention away from the appeal of possible rewards, and thus might be related to diminished working memory. For similar reasons we administered the Stroop task, per-

---

choose to transfer the money from the temporary bank at any time, facilitating the introduction of a new balloon. Herein lies the tension; the attraction of each additional cent must be played off against diminishing relative gains, and a steadily "ballooning" chance of loss. After being presented with ten balloons that last until the participant collects their winnings or the balloon explodes, risk-taking is indicated by the average number of pumps on all unexploded balloons (Lejuez et al., 2002). It was this score that was predicted by our measures of digit ratio.

formance on which has also been linked to the DLPFC, as well as the anterior cingulate cortex (ACC; Swick & Jovanovic, 2002). The ACC is also of interest, as it plays an important role in the detection and evaluation of rewards as well as goal-related conflicts (Fishbein et. al., 2005).

Surprisingly, we found that working memory actually improved in response to the highly attractive faces and similarly, interference in Stroop performance decreased. In a subsequent study, however, we found that attractive females caused impaired Stroop performance for low testosterone males but enhanced Stroop performance for high testosterone males. Nevertheless, in both cases the decrease in interference on the Stroop and the increase in working memory were apparent for those who played the balloon task in a riskier manner. So rather than providing evidence of a failing executive system, we found evidence of improved executive function co-occurring with an increase in risk-taking. Thus, in contrast with our initial hypothesis, these data suggest an alternative perspective: If you're going to sneak into the harem, you had better have your wits about you.

Having found what at first blush appeared to be counter-intuitive results in our application of both the Stroop and working memory tasks, we sought to pursue the function of the ventromedial pre-frontal cortex (VMPFC) as an alternative mediating mechanism. The VMPFC has been cited as integral to the somatic marker hypothesis (Bechara, 2004), according to which this neural region provides somatosensory feedback that influences decision making via homeostasis, emotion and feeling. Deficient functioning in this region has been linked to diminished emotional arousal and severe impairment in judgment

and decision making (Bechara et al., 1994). Patients with lesions to this region seem impervious to negative consequences incurred as a result of their poor decision making, apparently blinded by the pursuit of potential gains (Bechara et al., 1994). De-activation of the VMPFC might be a potential mechanism for the risky-shifts we had previously observed on the balloon task, as continued pumping of the balloon might be understood in terms of a deregulated sensitivity to the threat of looming punishment and/or a heightened sensitivity to reward. Importantly, the VMPFC has also been shown to be active in response to attractive, opposite sex faces (O'Doherty et al., 2003), suggesting that such activation might make people relatively insensitive to additional somatosensory feedback they might otherwise experience in response to risky decisions.

Aside from fMRI studies, there are a couple of alternative methods for exploring ventromedial function, the most common of which is the Iowa Gambling Task (Bechara et al., 1994). However, impaired performance on this task has also been found in patients with lesions to the dorsalateral PFC (Fellows & Farah, 2005), and thus we opted for the "reversal learning" task, which specifically targets the VMPFC (Fellows & Farah, 2005). Reversal learning involves choosing between two simple options (in our case two patterns simultaneously presented on a computer screen), one of which provides more rewards and fewer punishments, occurring in the form of monetary wins and losses. The task is simple, feedback is immediate and participants soon learn the relative value of the two choices. However, having done so, the contingencies are then switched and the participants' ability to adjust their choices accordingly becomes the measure of interest.

When we applied this measure in one of our studies that utilized the balloon task, we did indeed find reversal learning impairment for those exposed to the highly attractive faces. Furthermore, we found this effect to be significantly moderated by testosterone: after viewing the more attractive faces high testosterone males made more reversal learning errors and exercised less caution on the balloon task. Conversely, amongst low testosterone males, viewing the less attractive faces corresponded with more reversal learning errors and more risk-taking on the balloon task. While we were unable to show that reversal learning mediated the increased risk-taking found on the balloon task, this pattern is consistent with such a process. Thus, the possibility remains that VMPFC activation occurred in response to the attractive faces, and thereby diminished sensitivity to subsequent somatosensory feedback as the balloon threatened to explode.

Taken together these studies lend support to a functionally compartmentalized executive system that is sensitive to context, individual differences in testosterone, and possibly hormonal fluctuations. While further study is warranted, these studies provide preliminary support for the possibility of an evolved system that maximized reproductive success by desensitizing males to risk at the precise moment that such risks have the greatest potential reproductive payoff. In combination with the research described above on aging and disinhibition, the current set of studies provide an expanding picture of the role of executive functions in self-control across the lifespan.

References

Alexopoulos, G. S. (2003). Role of executive function in late-life depression. *Journal of Clinical Psychiatry, 64 [suppl 14],* 18-23.

Altemeyer, B. (2003). Why do religious fundamentalists tend to be prejudiced? *International Journal for the Psychology of Religion, 13,* 17-28.

Banfield, J.F., Wyland, C.L., Macrae, C.N., Munte, T.F., Heatherton, T.F. (2004). The cognitive neuroscience of self-regulation. In R.F. Baumeister & K.D. Vohs (Eds). *Handbook of self-regulation.* NY: Guilford.

Bechara, A. (2004). The role of emotion in decision making: Evidence from neurological patients with orbitofrontal damage. *Brain and Cognition, 55,* 30 - 40.

Bechara, A. D., Damasio, A. R., Damasio, H., & Anderson, S. W. (1994). Insensitivity to future consequences following damage to human prefrontal cortex. *Cognition, 50,* 7–15.

Bjorklund & Harnishfeger, (1995). Differences in parental investment contribute to important differences between men and women. *Current Directions in Psychological Science, 8, 3, 86 – 89.*

Buss, D., & Barnes, M. (1986). Preferences in human mate selection. *Journal of Personality and Social Psychology, 50,* 559 - 570.

Connelly, S. L., Hasher, L., & Zacks, R. T. (1991). Age and reading: The impact of distraction. *Psychology and Aging, 6,* 533-541.

Crandall, C. S., & Eshleman, A. (2003). A justification-suppression model of the expression and experience of prejudice. *Psychological Bulletin, 129,* 414-446.

Dabbs, J. M., & Dabbs, M. G. (2000). *Heroes, Rogues, and Lovers: Testosterone and Behavior*. New York: McGraw Hill.

Daly, & Wilson (2001). Risk-taking, intrasexual competition and homicide. *Nebraska Symposium on Motivation*, *47*, 1 - 36.

Daly, & Wilson (2005). Carpe diem: Adaptation and devaluing the future. *The Quarterly Review of Biology*, *80*, 55 - 61.

Daly, M., & Wilson, M. (2004). Do pretty women inspire men to discount the future? *Biology Letters, 271*, 177 - 179.

Davis, R. N., & Nolen-Hoeksema, S. (2000). Cognitive inflexibility among ruminators and nonruminators. *Cognitive Therapy & Research, 24*, 699-711.

Dekel, E., & Scotchmer, S. (1999). On the evolution of attitudes towards risk in winner-take-all games. *Journal of Economic Theory, 87*, 125-43.

Dempster, F. N. (1992). The rise and fall of the inhibitory mechanism: Toward a unified theory of cognitive development and aging. *Developmental Review, 12*, 45-75.

Devine, P.G. (1989). Stereotypes and prejudice: Their automatic and controlled components. *Journal of Personality and Social Psychology, 56*, 5-18.

Eigsti, I., Zayas, V., Mischel, W., Shoda, Y., Ayduk, O., Dadlani, M. B., Davidson, M. C., Aber, J. L., & Casey, B. J. (2006). Predictive cognitive control from preschool to late adolescence and young adulthood. *Psychological Science, 17*, 478-484.

Engle, R. W. (2002). Working memory capacity as executive function. *Current Directions in Psychological Science, 11*, 19 -23.

Fellows, L. K., & Farah, M. J. (2005). Different underlying impairments in decision-making following ventromedial and dorsolateral frontal lobe damage in humans. *Cere-*

bral Cortex, 15, 58 - 63.

Fishbein, D. H., Eldretha, D. L., Hyde, C., Matochik, J. A., London, E. D., Contoreggi, C., Kurian, V., Kimes, A.S., Breeden, A., Grant, S. (2005). Risky decision making and the anterior cingulate cortex in abstinent drug abusers and nonusers. *Cognitive Brain Research, 23*, 119 - 136.

Gangestad, S.W., Thornhill, R. & Yeo, R.A. (1994). Facial attractiveness, developmental stability and fluctuating asymmetry. *Ethology and Sociobiology, 15,* 73 – 85.

Hasher, L., & Zacks, R. T. (1988). Working memory, comp-rehension, and aging: A review and a new view. In G. H. Bower (Ed.), *The Psychology of Learning and Motivation: Vol 22* (pp. 193-225). San Diego, CA: Academic Press.

Hasher, L., Zacks, R. T., & May, C. P. (1999). Inhibitory control, circadian arousal, and age. In D. Gopher & A. Koriat (Eds.), *Attention & Performance, XVII, Cognitive Regulation of Performance: Interaction of Theory and Application* (pp. 653-675). Cambridge, MA: MIT Press.

Henry, J. D., von Hippel, W., & Baynes, K. (under review). Social inappropriateness and executive control in older adulthood.

Herek, G. M. (1994). Assessing heterosexuals' attitudes toward lesbians and gay men: A review of empirical research with the ATLG scale. In B. Greene & G. M. Herek (Eds.), *Lesbian and gay psychology: Theory, research, and clinical applications.* (pp 206-228).

Hertel, P. T. (1997). On the contribution of deficient cognitive control to memory impairment in depression. *Cognition and Emotion, 11*, 569-583.

Kane, M. J., & Engle, R. W. (2002). The role of the pre-frontal cortex in working memory capacity, executive function, and general fluid intelligence: And individual dif-

ferences perspective. *Psychonomic Bulletin and Review, 9,* 637 - 671.

Kramer, A.F., Hahn, S., Cohen, N.J., Banich, M.T., McAuley, E., Harrison, C.R., Chason, J., Vakil, E., Bardell, L., Boileau, R.A., & Colcombe, A. (1999). Aging, fitness and neurocognitive function. *Nature, 400,* 418-419.

Leigh, S. R. (1992). Patterns of variation in the ontogeny of primate body size dimorphism. *Journal of Human Evolution, 23,* 27 - 50.

Lejuez, C. W., Read, J. P., Kahler, C. W., Richards, J. B., Ramsey, S. E., Stuart, G. L., et al. (2002). Evaluation of a behavioral measure of risk taking: The Balloon Analogue Risk Task (BART). *Journal of Experimental Psychology: Applied, 8,* 75-84.

Lesieur, H.R. & Blume, S. (1987). The South Oaks Gambling Screen (SOGS): a new instrument for the identification of pathological gamblers. *American Journal of Psychiatry, 144,* 1184-1188.

Manning, J.T., Bundred, P.E., Newton, D.J., & Flanagan, B.F. (2003). The 2nd to 4th digit ratio and variation in the androgen receptor gene. *Evolution and Human Behavior, 24,* 399 - 405.

Manning, J.T., Scutt, D., Wilson, J., & Lewis-Jones, D.I. (1998). The Ratio of 2nd to 4th Digit Length: A predictor of sperm numbers and concentrations of testosterone, luteinizing hormone and oestrogen. *Human Reproduction, 13,* 3000 - 3004.

O'Doherty, J., Winston, J., Critchley, H., Perrett, D., Burt, D. M., & Dolan, R. J. (2003). Beauty in a smile: the role of medial orbitofrontal cortex in facial attractiveness. *Neuropsychologia, 41,* 147-55.

Pushkar, D., Basevitz, P., Arbuckle, T., Nohara-LeClair, M., Lapidus, S., & Peled, M. (2000). Social behavior and off-target verbosity in elderly people. *Psychology and Aging,*

15, 361-374.

Radvansky, G. A., Copeland, D., E., & von Hippel, W. (under review). Stereotype activation, inhibition, and aging.

Rogers, R. D., Ramnani, N., Mackay, C., Wilson, J. L., Jezzard, P., & Carter, C. S. (2004). Distinct portions of anterior cingulate cortex and medial prefrontal cortex are activated by reward processing in separable phases of decision-making cognition. *Biological Psychiatry*, *55*, 594– 602.

Roney, J. R. (2003). Behavioral and hormonal responses of men to brief interactions with women. *Evolution and Human Behavior*, *24*, 365 - 375.

Ryan, L., Hatfield, C., & Hofstetter, M. (2002). Caffeine reduces time-of-day effects on memory performance in older adults. *Psychological Science*, *13*, 68-71.

Schuman, H., Steeth, C., Bobo, L., Krysan, M. (1997). *Racial attitudes in America: Trends and interpretation*. Cambridge: Harvard University Press.

Swick, D., Jovanovic, J. (2002). The anterior cingulated cortex and the Stroop task: neuropsychological evidence for topographic specificity. *Neuropsychologia*, 40, 1240 – 1253.

Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Eds.), *Sexual Selection and the Descent of Man*. Chicago, Aldine-Atheron.

van Honk, J., Schutter, D., Hermans, E. J., Putmana, P., Tuitena, A., & Koppeschaar, H. (2004). Testosterone shifts the balance between sensitivity for punishment and reward in healthy young women. *Psychoneuroendocrinology*, *29*, 937 - 943.

von Hippel, W., & Dunlop, S.M. (2005). Aging, inhibition, and social inappropriateness. *Psychology and Aging*, *20*, 519-523.

von Hippel, W., & Gonsalkorale, K. (2005). “That is bloody revolting!” Inhibitory control of thoughts better left unsaid. *Psychological Science, 16,* 497-500.

von Hippel, W., Ng, L., Caldwell, S., Gill, G., Abbott, L., & Powell, K. (under review). Deficits in executive functioning predict problem gambling in older adults.

von Hippel, W., Radvansky, G. A., & Copeland, D. C. (under review). The nature of age differences in prejudice toward gay men, working women, and Blacks.

von Hippel, W., Silver, L.A., & Lynch, M.E. (2000). Stereotyping against your will: The role of inhibitory ability in stereotyping and prejudice among the elderly. *Personality and Social Psychology Bulletin, 26,* 523-532.

von Hippel, W., Vasey, M.W., Gonda, T., & Stern, T. (in press). Executive function deficits, rumination, and late-onset depressive symptoms in older adults. *Cognitive Therapy & Research.*

West, R. L. (1996). An application of prefrontal cortex function theory to cognitive aging. *Psychological Bulletin, 120,* 272-292.

Whitmer, A. J., & Banich, M. T. (2007). Inhibition versus switching deficits in different forms of rumination. *Psychological Science.*

Wilson, M., & Daly, M. (1985). Competitiveness, risk taking, and violence: The young male syndrome. *Ethology and Sociobiology, 6,* 59-73.

Wilson, T. C. (1996). Cohort and prejudice: Whites' attitudes toward Blacks, Hispanics, Jews and Asians. *Public Opinion Quarterly, 60,* 253-274.

Winocur, G., & Hasher, L. (2004). Age and time-of-day effects on learning and memory in a non-matching-to-sample test. *Neurobiology of Aging, 25,* 1107-1115.

Zerjal, T., Wells, R. S., Yuldasheva, N., Ruzibakiev, R., & Tyler-Smith, C. (2003). A genetic landscape reshaped by recent events: Y-chromosomal insights into central Asia. *American Journal of Human Genetics*, *71*, 466 - 482.

Zuckerman, M. (1994). *Behavioural expressions and biological bases of sensation seeking*. Cambridge; New York: Cambridge University Press.