Hormones and Behavior xxx (2016) xxx–xxx

Contents lists available at ScienceDirect

Hormones and Behavior

journal homepage: www.elsevier.com/locate/yhbeh

Review article

The Point Subtraction Aggression Paradigm as a laboratory tool for investigating the neuroendocrinology of aggression and competition

Shawn N. Geniole [a], Elliott T. MacDonell [a], Cheryl M. McCormick [a,b,*]

[a] Department of Psychology, Brock University, 1812 Sir Isaac Brock Way, St. Catharines, Ontario L2S 3A1, Canada
[b] Centre for Neuroscience, Brock University, 1812 Sir Isaac Brock Way, St. Catharines, Ontario L2S 3A1, Canada

ARTICLE INFO

Article history:
Received 18 December 2015
Accepted 15 April 2016
Available online xxxx

Keywords:
Costly aggression
Social neuroendocrinology
Sex differences
Competition
Testosterone
Cortisol
Estradiol

ABSTRACT

A contribution to a special issue on Hormones and Human Competition. The ease of measuring steroids in saliva has led to an increase in investigating their role in competition and aggression in laboratory settings and using behavioral measures of aggression. We review here the Point-Subtraction-Aggression-Paradigm (PSAP) as a measure of costly aggression and we compare and contrast the PSAP to other aggression measures. We describe our use of the PSAP, highlighting how it can be modified to investigate a broad array of experimental questions. We review studies that have investigated neuroendocrine function and the PSAP, and we conclude that across studies the relationship between fluctuations in testosterone and PSAP aggression scores are directionally positive, and are likely specific to men. Investigations of other neuroendocrine measures and the PSAP are fewer, limiting conclusions that can be drawn for other hormones. We provide two versions of the PSAP that can be used with E-PRIME® software for researchers interested in this measure for their laboratories.

Contents

Introduction

From the perspective of behavioral ecology and ethology, aggression among conspecifics occurs primarily as the result of competition for limited resources, be they food, shelter, or mating opportunities.

* Corresponding author at: Centre for Neuroscience, Department of Psychology, Brock University, 1812 Sir Isaac Brock Way, St. Catharines, Ontario L2S 3A1, Canada.
E-mail address: cmccormick@brocku.ca (C.M. McCormick).

http://dx.doi.org/10.1016/j.yhbeh.2016.04.006
0018-506X/

Aggression that occurs in the context of the formation of dominance hierarchies also involves the objective of attaining greater access to, and control of, limited resources. Aggression is often cast as the mechanism of competition (e.g., Walls and Jaeger, 1987) or as the requisite for the occurrence of competition (e.g., Schuster, 1983), indicating the high conceptual overlap between the terms aggression and competition. Further, although aggression has been cast as maladaptive and antisocial, when considered in the context of competition, there is much evidence for aggression as a form of social competence (e.g., Hawley, 2007; Pellegrini, 2007; Faris and Felmlee, 2011). For example, aggression is used by some individuals to achieve interpersonal goals (e.g., status attainment and maintenance), and aggression can increase likeability by peers (reviewed in Hawley and Vaughn, 2003; Sutton et al., 1999).

The neuroendocrine systems that support competitive, aggressive behavior have been investigated in field and laboratory studies in a wide variety of species, with androgenic hormones identified as having a prominent role (e.g., Rosvall, 2013; Gleason et al., 2009; Mazur, 2006; Soma et al., 2015). The advent of non-invasive means of measuring testosterone in saliva samples (Granger et al., 2004) has led to an increase in investigations of hormone-competition relationships in people. Further, the ease of sampling allows for investigation of shifts in testosterone concentrations before, during, and after an aggressive event. Several behavioral measures of aggression are available for use in laboratory studies (Taylor Aggression Paradigm, Taylor, 1967; Hot Sauce Paradigm, Lieberman et al., 1999; Voodoo Doll Task, DeWall et al., 2013), allowing researchers to move beyond self-report data, and with experimental controls not possible in field studies. In this review, we describe the Point Subtraction Aggression Paradigm (PSAP) as a laboratory measure of aggression and competitive interaction, its reliability and validity as a measure, and compare and contrast the PSAP with other lab measures of aggression. We describe our use of the PSAP, highlighting how the PSAP can be modified to investigate specific questions, and how the PSAP has been used to investigate neuroendocrine-aggression relationships.

The PSAP as a measure of aggression and competition

The PSAP was designed by Cherek (1981) and is guised as an online computer game that participants play against a fictitious opponent. Participants are told that the goal of the game is to earn as many points as possible and that all points earned will be exchangeable for money at the end of the task, providing a monetary incentive for participants to earn points. Based on our university's Research Ethics Board, however, we provide all participants with the same sum at the end of the game, a sum that is greater than the maximal exchange possible based on the specific version of the PSAP involved. To earn a point, participants must press a predetermined key on a keyboard a set number of consecutive times (typically, participants earn one point for every 100 consecutive presses). Participants are informed that they may see their point counter flash several times in red font and their point total decrease, and that the decrease is because the other player has stolen a point from them. Participants are told that they can respond to this provocation in one of three ways: they can continue to earn points by pressing the same key, they can begin pressing a second key, which protects their points for a variable amount of time, or they can begin pressing a third key, which functions to steal points from the other player. Participants are told that they have been randomly assigned to the condition in which they do not get to keep any of the points they steal from the other player (i.e., steals decrease the other player's point counter, but do not increase the participant's point counter). Therefore, stealing does not benefit the participant financially, and, because stealing represents a behavior intended to cause (financial) harm to another individual who would rather avoid such treatment, it is consistent with the definition of aggression of Baron and Richardson (1994), whereby aggression is any act intended to harm another individual who would rather avoid such treatment; further, the harm need not be physical (e.g., aggression can be indirect, relational, or financial), but must lead to some aversive consequence for the recipient. Researchers thus use the number of steals in the PSAP as a behavioral index of aggression in the laboratory.

Although the PSAP is not explicitly framed as a competition between the participant and the fictitious player insofar as we never mention "winning" and "losing", and there are no monetary benefits associated with obtaining more points than the other player during the instructions, participants still view the task as competitive, often asking if they earned more points than the other participant. We have previously argued that although the PSAP is not a conventional form of competition, it involves competition in that the reward earned depends on performance (number of button presses) and strategy (which buttons are pressed) of the player as well as the performance of the opponent (number of provocations) (Carré and McCormick, 2008). Although some of the aggression in the PSAP may be derived from the strategy of competition, the significant increase in its use after provocation suggests that it is reactive aggression.

Is the PSAP a reliable and valid measure of aggression?

Although the original version of the PSAP involves multiple rounds of "gameplay" each lasting 25 to 60 min (e.g., Cherek, 1981; Cherek et al., 1997), a single 25-minute round maintains good psychometric properties (i.e., shares correlations with other measures of aggression, Golomb et al., 2007), and steal presses in one 25-minute round are correlated with those of other rounds within a single testing session (Bailly and King, 2006). We developed a version of the PSAP that involves three 12-minute rounds (Carré and McCormick, 2008) that maintains participant motivation (as indexed by total button presses, which do not decrease significantly from round to round).

The PSAP also appears to possess good test-retest reliability. For example, McCloskey et al. (2005) administered two different versions of the PSAP to participants at two different time points that were an average of 62 days apart (McCloskey et al., 2005). In the first version of the task, which was administered during the first testing session, the protect response option was not available to select; in the second version of the task, which was administered during the second testing session, it was available to select. Despite the change in task parameters across the two testing sessions, the number of steal presses in the first testing session was highly correlated with that of the second testing session ($r = 0.74$). Therefore, in addition to being internally consistent, and reliably tapping into behavior during brief testing sessions, the PSAP also appears to possess good test-retest reliability across longer time spans.

The PSAP has been well-validated (for an earlier review, see Cherek et al., 2003). For example, participants who steal more in the PSAP tend to have higher scores on other measures of aggression and hostility (see Table 1). The associations between steal presses in the PSAP and other measures of aggression are directionally positive in almost all cases, but vary in statistical significance and magnitude, likely because some of the studies involved small samples (i.e., were underpowered, Lieving et al., 2008; Tcheremissine et al., 2005) and because the other aggression measures may tap into aspects of aggression broader than that captured by the PSAP. For example, when the total score of the Life History of Aggression Scale (LHAS; Coccaro et al., 1997) is used, it shares weak and non-significant associations with steal presses in the PSAP (Golomb et al., 2007; Marsh et al., 2002). When the individual factors of the LHAS are examined, however, the PSAP shares stronger associations with the aggression factor (rs 0.20 to 0.50, Coccaro et al., 1996; McCloskey et al., 2009) than with the self-aggression factor ($r = 0.03$ in McCloskey et al., 2009, *ns* in Coccaro et al., 1996). Similarly, the PSAP appears to better capture the aggressiveness/assault and irritability factors of the Buss-Durkee Hostility Inventory (Buss and Durkee, 1957) than the other factors of the Inventory (e.g., Cherek et al., 2000). Based on the correlations provided in Table 1, the PSAP appears to share the most consistent and strong associations with the aggressiveness/assault and irritability subscales (mean rs, weighted by sample sizes: 0.53, 0.53)

Please cite this article as: Geniole, S.N., et al., The Point Subtraction Aggression Paradigm as a laboratory tool for investigating the neuroendocrinology of aggression and competit..., Horm. Behav. (2016), http://dx.doi.org/10.1016/j.yhbeh.2016.04.006

Table 1
Associations between the PSAP steal presses and other measures of aggression.

r^a with PSAP aggression	N Men	N Women	N All	Participant details	Reference
Brown History of Violence (Brown et al., 1979)					
0.44	12			Violent and non-violent parolees	Cherek et al. (1996)
0.72	30			Violent and non-violent parolees	Cherek et al. (1997)
0.36		30		Violent and non-violent parolees	Cherek et al. (2000)
ns		30		Healthy volunteers, Borderline Personality Disorder	Dougherty et al. (1999)
Life History of Aggression (LHA) (Coccaro et al., 1997)					
0.07	56	44		Healthy volunteers	Golomb et al. (2007)
ns	10			Parolees and probationers	Lieving et al. (2008)
ns	6			History of conduct disorder	Tcheremissine et al. (2005)
ns		12		Healthy volunteers	Marsh et al. (2002)
LHA: aggression factor					
0.20			261	Healthy volunteers, Bipolar Disorder, other personality disorder (non-cluster B)	McCloskey et al. (2009)
0.49; 0.50	14			DSM-III-R Personality Disorders	Coccaro et al. (1996)
LHA: self-aggression factor					
0.03			261	Healthy volunteers, Bipolar Disorder, other personality disorder (non-cluster B)	McCloskey et al. (2009)
ns; *ns*	14			DSM-III-R Personality Disorders	Coccaro et al. (1996)
LHA: antisocial behavior and consequences of aggressive behavior factor					
0.13			261	Healthy volunteers, Bipolar Disorder, other personality disorder (non-cluster B)	McCloskey et al. (2009)
0.52; 0.49	14			DSM-III-R Personality Disorders	Coccaro et al. (1996)
Buss-Durkee Hostility Inventory (BHI) (Buss and Durkee, 1957)					
0.36	30			Violent and non-violent parolees	Cherek et al. (1997)
0.35; 0.16		30		Violent and non-violent parolees	Cherek et al. (2000)
0.44		30		Healthy Volunteers, Borderline Personality Disorder	Dougherty et al. (1999)
BHI: direct aggressiveness/assault scale					
0.54	30			Heroin dependent patients	Gerra et al. (2007)
0.64	40			Heroin addicts and controls	Gerra et al. (2004)
0.63	12			Ecstasy users	Gerra et al. (2001)
0.78	20			Healthy volunteers	Gerra et al. (2001)
0.41; 0.33		30		Violent and non-violent parolees	Cherek et al. (2000)
0.04; 0.19	14			DSM-III-R Personality Disorders	Coccaro et al. (1996)
BHI: irritability scale					
0.63	30			Heroin dependent patients	Gerra et al. (2007)
0.60	40			Heroin addicts and controls	Gerra et al. (2004)
0.56	12			Ecstasy users	Gerra et al. (2001)
0.64	20			Healthy volunteers	Gerra et al. (2001)
0.33; 0.14		30		Violent and non-violent parolees	Cherek et al. (2000)
BHI: verbal scale					
0.32; 0.28		30		Violent and non-violent parolees	Cherek et al. (2000)
BHI: indirect scale					
0.22; 0.16		30		Violent and non-violent parolees	Cherek et al. (2000)
BHI: resentment scale					
0.20; −0.03		30		Violent and non-violent parolees	Cherek et al. (2000)
BHI: suspicion scale					
0.19; 0.19		30		Violent and non-violent parolees	Cherek et al. (2000)
BHI: negative scale					
−0.03; −0.01		30		Violent and non-violent parolees	Cherek et al. (2000)
BHI: guilt scale					
0.09; 0.01		30		Violent and non-violent parolees	Cherek et al. (2000)
Buss-Perry Aggression Questionnaire (BPAQ) (Buss and Perry, 1992)					
ns	10			Parolees and probationers	Lieving et al. (2008)
0.17			67	Controls, parolees, and probationers	Gowin et al. (2013)
ns	6			History of conduct disorder	Tcheremissine et al. (2005)
ns		12		Healthy volunteers	Marsh et al. (2002)
0.28	27	42		Undergrads	Herr et al. (2015)
ns	22	16		Bipolar Disorder patients with Intermittent Explosive Disorder	New et al. (2009)
ns	18	18		Healthy volunteers	New et al. (2009)
BPAQ: physical aggression scale					
0.20			323	Healthy volunteers, Bipolar Disorder, other personality disorder (non-cluster B)	McCloskey et al. (2009)
BPAQ: verbal aggression scale					
0.10			323	Healthy volunteers, Bipolar Disorder, other personality disorder (non-cluster B)	McCloskey et al. (2009)
BPAQ: anger scale					
0.18			323	Healthy volunteers, Bipolar Disorder, other personality disorder (non-cluster B)	McCloskey et al. (2009)
BPAQ: hostility scale					

(continued on next page)

Table 1 (*continued*)

r[a] with PSAP aggression	*N* Men	Women	All	Participant details	Reference
0.20			323	Healthy volunteers, Bipolar Disorder, other personality disorder (non-cluster B)	McCloskey et al. (2009)
Overt Aggression Scale (Yudofsky et al., 1986)					
0.73	30			Violent and non-violent parolees	Cherek et al. (1997)
0.06	12	16		Healthy volunteers and participants with histories of physical abuse	Moe et al. (2004)
Retrospective Overt Aggression Scale (ROAS) (Sorgi et al., 1991)					
0.28; **0.36**		30		Violent and non-violent parolees	Cherek et al. (2000)
ns		30		Healthy Volunteers, Borderline Personality Disorder	Dougherty et al. (1999)
ROAS: verbal scale					
0.32; 0.28		30		Violent and non-violent parolees	Cherek et al. (2000)
ROAS: objects scale					
0.03; 0.12		30		Violent and non-violent parolees	Cherek et al. (2000)
ROAS: self scale					
0.26; 0.24		30		Violent and non-violent parolees	Cherek et al. (2000)
ROAS: others scale					
0.38; 0.52		30		Violent and non-violent parolees	Cherek et al. (2000)
State-Trait Anger Expression Inventory (SAEI) (Spielberger and Sydeman, 1994)					
ns	22	16		Bipolar Disorder patients with Intermittent Explosive Disorder	New et al. (2009)
ns	18	18		Healthy volunteers	New et al. (2009)
SAEI: state anger scale					
0.45	22	16		Bipolar Disorder patients with Intermittent Explosive Disorder	New et al. (2009)
0.07			276	Healthy volunteers, Bipolar Disorder, other personality disorder (non-cluster B)	McCloskey et al. (2009)
SAEI: trait anger					
0.16			276	Healthy volunteers, Bipolar Disorder, other personality disorder (non-cluster B)	McCloskey et al. (2009)
SAEI: anger in scale					
0.13			276	Healthy volunteers, Bipolar Disorder, other personality disorder (non-cluster B)	McCloskey et al. (2009)
SAEI: anger out scale					
0.18			276	Healthy volunteers, Bipolar Disorder, other personality disorder (non-cluster B)	McCloskey et al. (2009)
SAEI: anger control scale					
−0.16			276	Healthy volunteers, Bipolar Disorder, other personality disorder (non-cluster B)	McCloskey et al. (2009)
SAEI: anger expression scale					
0.19			276	Healthy volunteers, Bipolar Disorder, other personality disorder (non-cluster B)	McCloskey et al. (2009)
Conflict Tactics Scale (Straus, 1979)					
0.27	56	44		Healthy volunteers	Golomb et al. (2007)
Statin Study Questionnaire-Conflict (Golomb et al., 2007)					
0.26	56	44		Healthy volunteers	Golomb et al. (2007)
International Personality Item Pool (IPIP) (Goldberg et al., 2006)					
IPIP: anger subscale					
−0.02			56	Undergrads and postgraduate students	Pinto et al. (2012)
IPIP: trait dominance subscale					
ns	37			Undergrads	Carré et al. (2009)
ns		51			
Minnesota Multiphasic Personality Inventory (MMPI) (Friedman et al., 1989)					
MMPI: psychopathic deviate scale					
0.25	100			Violent offenders and controls	Zhou et al. (2006)
0.45	40			Heroin addicts and controls	Gerra et al. (2004)
MMPI: paranoia scale					
0.08	100			Violent offenders and controls	Zhou et al. (2006)

[a] In some cases, the authors used more than one measure of PSAP aggression (e.g., steal presses/total presses; steal presses/min). In such cases, we report both correlations and separate them with a semicolon. All measures reported here involved steal presses that occurred during a PSAP round in which the participant was provoked or, in one case (New et al., 2009), a difference score representing PSAP steals in a round in which participants were provoked, subtracted by PSAP steals in a round in which participants were not provoked. Thus, all measures reported here represent reactive rather than proactive aggression. Correlations in bold were reported as significant in the corresponding manuscripts.

of the Buss-Durkee Hostility Inventory, relative to the other measures of aggression. Example items from the aggressiveness/assault subscale include “I get into fights about as often as the next person”, “People who continually pester you are asking for a punch in the nose”, “Once in a while I cannot control my urge to harm others”, “If somebody hits me first, I let him have it”, whereas example items from the irritability subscale include “I often feel like a powder keg ready to explode”, “I am irritated a great deal more than people are aware of”, “I sometimes carry a chip on my shoulder”, and “It makes my blood boil to have somebody make fun of me”. Steal presses in the PSAP may thus best index aggressive behavior that is both physical and direct, and that results from both general irritability, and heightened irritability in response to provocation.

Please cite this article as: Geniole, S.N., et al., The Point Subtraction Aggression Paradigm as a laboratory tool for investigating the neuroendocrinology of aggression and competit..., Horm. Behav. (2016), http://dx.doi.org/10.1016/j.yhbeh.2016.04.006

In addition to its associations with self-report and observer report measures of behavior, the PSAP also discriminates between groups that are expected to differ in aggressiveness. For example, parolees with a history of violence or those who were convicted of violent crimes (e.g., assault, aggravated assault, aggravated robbery) stole more during the PSAP than did parolees without a history of violence or parolees who were convicted of non-violent crimes (e.g., theft, burglary, forgery, drug offences) (Cherek et al., 1996; Cherek et al., 2000; Cherek et al., 1997). Similarly, participants with Borderline Personality Disorder (Dougherty et al., 1999; McCloskey et al., 2009), Antisocial Personality Disorder (Moeller et al., 1997), and Intermittent Explosive Disorder (New et al., 2009), stole more points in the PSAP than did participants without these disorders. Therefore, the PSAP appears to be a valid index of aggressiveness, correlating positively with other self- and observer-report measures of aggression and discriminating between groups that typically vary in aggressiveness.

Participants' responses to provocation and their self-reported thoughts during the task also support the idea that steal presses in the PSAP represent a valid index of aggressive behavior. For example, provocation significantly increases the use of retaliatory steal presses in the PSAP (Geniole et al., 2011; Geniole et al., 2015; McCloskey et al., 2005; New et al., 2009), and provocation is known to be an important predictor of aggressive behavior (Anderson and Bushman, 2002; Buss, 1961). We typically include two open-ended questions to assess participants' thoughts about the task and the other fictitious player ("What were your thoughts about your competitor? While playing, did you form an impression of your competitor, either positive or a negative impression? If so, please describe your impression in a sentence or two" and "General comments"). Participants have reported that they "would get irritated" and were "frustrated for having to get the lost points back" and that "the opponent was making [them] angry". They reported that they had "formed a negative impression about [the] competitor because they kept stealing points", that he/she "was rather aggressive" and "just nasty [for] stealing away all [of the] hard earned points". During the task, participants thought about "attacking the opponent" and "hurting the other player". Although these comments are from a subset of participants and may not reflect the thoughts of all individuals who perform the task, they nonetheless bolster the idea that point subtractions in the PSAP are irritating, frustrating, and thus provoking to some participants. The comments also support the idea that the provocations in the PSAP increase some participants' anger and promote the desire to attack and hurt the other player. Therefore, the increase in steal presses, negative attitudes, and desire to harm the other player after provocation adds further support to the validity of the PSAP competition as a measure of behavioral aggression.

It is also possible that some of the variation in PSAP steal presses is motivated by other factors that may even be prosocial in nature, such as reciprocity or distributive justice (Tedeschi and Quigley, 1996). Nevertheless, participants retaliate at a rate far greater than a simple tit-for-tat strategy (see Fig. 2 in Tedeschi and Quigley, 1996; on average the rate of retaliation is double that of the number of provocations). Thus, it appears that reciprocity or distributive justice motives may explain some but not all of participants' motivations for stealing during the task. Another possibility is that participants steal points, in part, because of boredom during the task, although boredom would likely lead to an increase in all types (i.e., a variety) of button presses. Although no studies to date have examined directly the relationship between boredom during the task and PSAP steal presses, some researchers have examined experimental effects on multiple button presses (e.g., McCloskey et al., 2005) to rule out potential boredom effects. If effects are specific to steal presses, and not other types of button presses, such an analysis might provide some assurance that the effects were not solely caused by boredom; such a relationship was found in Carré and McCormick (2008), whereby only steal presses were associated with testosterone concentrations.

How is the PSAP different from other behavioral measures of aggression?

The PSAP includes a non-aggressive response option

Competitive and provocative interactions in the real world typically allow for both aggressive and non-aggressive response options. Aggression measures that do not include both of these types of responses may thus have limited ecological validity and/or may misrepresent the construct of aggression (Tedeschi and Quigley, 1996). For example, individuals who would normally avoid confrontation, flee from a conflict, or protect themselves in some way rather than retaliate against an individual who has provoked them, may be guided towards retaliation in laboratory tasks that include only an aggressive response option. The original version of the PSAP included only an "earn" and a "retaliate" response option (Cherek, 1981), and the "point-protection" response option was added in later versions. When this additional protection option was introduced into the PSAP (Allen et al., 1996), participants still retaliated to provocation by stealing points, but the extent of their retaliation was far less than when they did not have this additional non-aggressive response option (McCloskey et al., 2005). Thus, designs lacking non-aggressive responses options may bias participants towards greater aggressiveness, and the inclusion of the protection response option reduces demand characteristics in the PSAP, possibly increasing its ecological validity.

In the Taylor Aggression Paradigm (originally developed by Taylor, 1967) and later modified by others (reviewed in Giancola and Parrott, 2008), participants compete in several rounds of a reaction time task in which the winner of each round can choose the intensity and duration of a noxious stimuli (typically a shock or noise blast) to administer to the loser. This task often is administered without the inclusion of a non-aggressive response option. When researchers do include such an option in the task, the option typically involves the forfeiting of a response (i.e., participants lose their opportunity to deliver the noxious stimuli to the opponent). Because the only behavioral response available to participants is an aggressive one, delivering the noxious stimuli may represent the desire to provide a behavioral response, more generally, rather than to provide an aggressive response, specifically. Similarly, in the Hot Sauce Paradigm (Lieberman et al., 1999) in which participants can decide the amount and spiciness of hot sauce that another participant averse to spicy food must consume, and in the Voodoo Doll Task (DeWall et al., 2013) in which participants prick dolls representing other individuals, non-aggressive response options are either not possible or they involve forfeiting the opportunity to provide any behavioral response. As a consequence, these tasks may overestimate participants' aggressiveness by funnelling their responses towards this form of behavior.

In future studies, it may be beneficial to examine directly the extent to which these changes in PSAP parameters moderate the associations between steal presses and other behavioral and self-report measures of aggression, as such analyses would provide additional insight into the validity of versions of the PSAP with and without non-aggressive response options.

In the PSAP, aggression is costly

Many researchers have emphasized the importance of cost-benefit analysis in models of competition and aggression (e.g., Archer et al., 2010; Archer and Southall, 2009; Campbell, 1999; Georgiev et al., 2013; Griskevicius et al., 2009; Rutter and Hine, 2005). In day to day situations, for example, acting aggressively may benefit an individual by helping them assert their dominance and secure their position in a status hierarchy, but such behavior often comes at costs that are both tangible (e.g., lawsuits, fines, jail time) and intangible (e.g., fear of retaliation). As a consequence, the decision to act aggressively may involve the weighing and consideration of costs and benefits, either

Please cite this article as: Geniole, S.N., et al., The Point Subtraction Aggression Paradigm as a laboratory tool for investigating the neuroendocrinology of aggression and competit..., Horm. Behav. (2016), http://dx.doi.org/10.1016/j.yhbeh.2016.04.006

consciously or subconsciously. In the PSAP, aggressive responses are made at a tangible cost to participants; stealing points does not increase the participants' point tally and instead detracts from pressing the button to earn points. Participants who steal more frequently during the task earn less than those who steal less frequently (e.g., Carré and McCormick, 2008; Carré et al., 2009; Geniole et al., 2011; Pinto et al., 2012). The costliness of stealing in the PSAP is a critical feature – not just for understanding how cost-benefit analysis may guide aggression – but also for maintaining ecological validity; without some costs associated with aggression, certain laboratory measures may overestimate levels of aggression that would occur outside of the laboratory. For example, in the Hot Sauce Paradigm and the Voodoo Doll Task, participants have the opportunity to aggress without any tangible costs. In the Taylor Aggression Paradigm (and its variants), although there are no tangible costs to retaliation, participants may fear a retaliatory noise blast.

What motivates aggression in the PSAP?

Because acting aggressively in the PSAP is costly to personal earnings, this retaliatory behavior may also be driven by poor economic decision-making (poor cost-benefit analysis). In this respect, the PSAP has much in common with the Ultimatum Game, in which one participant (the proposer) is given a sum of money and decides the amount of the sum to offer another participant (the responder). If the responder accepts the sum offered, both participants obtain their respective allotments, but if the responder rejects the offer, neither receives any of the sum. The rational economic choice for the responder is to accept any offer made by the proposer; nevertheless, as offers become lower, the rejection of offers increases (e.g., Güth et al., 1982; Rilling and Sanfey, 2011). Lower offers are provoking when they are deemed to be unfair; a responder will accept a randomly generated low offer that would not be accepted when offered as a decision made by a proposer (reviewed in Gabay et al., 2014). Costly punishment is driven, in part, by negative emotional reactions to a perceived provocation (Sanfey et al., 2003; Yamagishi et al., 2009), and costly punishment may have intrinsic reward value (e.g., Crockett et al., 2013). We have proposed that the motivation for costly punishment in the PSAP is similar to that in the Ultimatum Game; in both, the short-term financial costs of retaliation may be out-weighed by long-term emotional benefits and/or the possibility of influencing future social interactions (Carré et al., 2009).

The extrinsic financial costs of responding to provocation in the PSAP are likely offset by intrinsic rewards. Some evidence to support this possibility came from a study in which we modified the PSAP to create four conditions in a 2 × 2 factorial design (Carré et al., 2010). During the PSAP game, participants were either provoked or not and were either financially rewarded or not when they retaliated (i.e., they were either able or not able to keep the points they stole) (the provocation + no financial reward condition is most like the standard PSAP game). The number of button presses to earn, steal, or to protect points was set at 50, 50, and 50 as opposed to the 100, 10, and 10 of the standard PSAP to ensure that in the conditions whereby points stolen were kept (financial reward conditions) it was never easier to earn points by using the "steal" press option than it was to earn points by using the point press option. Participants reported higher levels of enjoyment of the PSAP game when their retaliation came at a financial cost than when it came with a financial reward (Carré et al., 2010). Further, we found a positive association between participants' enjoyment of the PSAP and their use of costly punishment only in the condition in which participants were provoked and retaliation was costly (Carré et al., 2010). In addition, only in this costly retaliation condition were participants biased towards choosing to engage in a subsequent competitive rather than non-competitive task. We have also found a positive association between participants' enjoyment of the PSAP and their use of costly punishment in the more standard version of the PSAP game (Geniole et al., 2011). Thus, although stealing points in the PSAP seems irrational in that it works against participants' economic self-interest (stealing points detracts from earning points, leading to lower payouts), these extrinsic costs appear to be offset by the intrinsic reward associated with retaliation.

Neuroimaging studies of economic exchange games show a relationship between costly punishment of unfair behavior and neural structures associated with reward processing such as the dorsal and ventral striatum (De Quervain et al., 2004; Singer et al., 2006; Crockett et al., 2013). Others, however, have argued that these activations may simply represent the organization of an aggressive response (White et al., 2014). There have been a few neuroimaging studies of aggressive responding in the PSAP using versions modified for functional magnetic resonance imaging, with not much consistency in neural regions reported to be associated with PSAP performance. For example, one study found a positive association between retaliation and increased activation in the ventral anterior cingulate cortex and the temporoparietal junction (Bubenzer-Busch et al., 2015), another reported a positive association between costly retaliation and neural activations in the amygdala, insula, and prefrontal cortex and significant striatal activity to both winning and losing points (Skibsted et al., 2015), and another found a negative relationship between costly retaliation and activity in the orbitofrontal cortex, prefrontal cortex, caudate, thalamus, and middle temporal gyrus (Kose et al., 2015). Some evidence, however, suggests that brain function during PSAP play may depend on genetic differences such as monoamine oxidase (an enzyme responsible for degradation of catecholamines and serotonin) tandem repeat promoter polymorphism (Schlüter et al., 2016), and there is evidence that MAOA-L carriers (genetic variant associated with lowered monoamine oxidase A expression) show more costly retaliation in the PSAP than do MAOA-H carriers (higher MAOA expression) (Gallardo-Pujol et al., 2013; Kuepper et al., 2013). Nevertheless, the pattern of neural activations during PSAP play remains difficult to interpret.

We recently investigated the motivations that promote costly aggression more directly by introducing other modifications to the PSAP game (Geniole et al., 2015). We considered the possibility that an individual's costly retaliation to provocation is not necessarily based in the tangible cost (i.e., absolute or literal financial costs) of the provocation incurred by the individual, but that the provocation may target intangible costs, and these costs may be more important in motivating retaliation. We considered an evolutionary perspective, that competition is an important driver of evolution, and that threats to social status are an important factor in retaliation by men based on the relationship between status and mating opportunities (Daly and Wilson, 1988). For example, a provocation, irrespective of the tangible costs (financial loss), might reflect a threat to status (intangible cost), and thus motivate aggressive responding in men, who may be more sensitive to threats to status than women, irrespective of the financial losses associated with the provocations. In contrast, women's greater parental investment than men's may render women more sensitive to the tangible costs associated with a provocation (i.e., the financial loss) (Campbell, 1999). Because threats to status and resources are tightly linked, we had to alter the PSAP to manipulate (orthogonally, or independently) these tangible and intangible costs. The effect of being provoked, in and of itself (which carries the intangible costs such as status loss), was separated from the financial loss associated with the provocations (the tangible cost) by randomly assigning participants to one of four conditions in which the number of provocations (10 vs 20) and the total financial loss associated with the provocations (10 vs 20 total points) varied. In this 2 (number of provocations) by 2 (total number of points lost) design, participants were either provoked 10 times, losing either 1 or 2 points per provocation (leading to total financial loss of either 10 or 20 points), or were provoked 20 times, losing either 0.5 or 1 point per provocation (leading to total financial loss of 10 or 20 points).

In addition, we also included a measure of proactive aggression in the PSAP, the number of steals made by the participant in the initial 45 s of the round, an interval that always preceded the first provocation by the (fictitious) opponent (Geniole et al., 2015). Researchers distinguish between two different subtypes of aggression (reviewed in Berkowitz, 1993; Dodge and Coie, 1987): proactive aggression, which often occurs in the absence of emotion, involves low autonomic arousal, and is often premeditated, goal oriented, and unprovoked, and; reactive aggression, which is emotionally driven and occurs in response to provocation or threat, often without regard for a goal (for a review of the correlates of both forms of aggression, see Cima and Raine, 2009). The inclusion of a measure of proactive aggression provides an important control for individual differences and allows the aggression specific to the provocation to be better identified. For example, although the total number of PSAP steals at the end of a round are likely to represent acts of reactive aggression that occur in response to provocation, it is possible that some of the presses occurred before the participant was provoked, more accurately reflecting proactive aggression. By examining both time points in a repeated-measures design (steals before vs after the first provocation), we can better isolate reactive aggression, or the increase in aggression that results from the provocation. Using this approach, we found that women showed the greatest increases in aggression when the cost incurred by the provocations was high rather than low, irrespective of the number of times they were provoked throughout the session. In contrast, men showed the greatest increases when they were provoked more rather than less frequently, irrespective of how much money they lost from the provocations (Geniole et al., 2015). These results supported the prediction that women would be more sensitive to the tangible cost of a provocation whereas men would be more sensitive to the intangible costs associated with provocations, which might reflect losses to status.

In the second experiment, to more directly examine the extent to which participants' retaliation was motivated by these intangible (status loss) versus tangible (financial loss) costs associated with provocation, participants were asked to reported the extent to which costly retaliation was used to protect their status or their financial resources in the task (Geniole et al., 2015). Women who reported using retaliation to protect their financial resources used more costly punishment (stole more points in retaliation) than did women who reported using retaliation to protect their status, and men who reported using retaliation to protect their status used more costly punishment than did men who reported using retaliation to protect their financial resources. Thus, behavior in the PSAP (steal presses) indicates that costly retaliation is motivated differentially in men and in women by intangible costs (threats to status) and by tangible costs (threats to financial resources) associated with the provocations.

Factors to consider when conducting PSAP studies

Deception

The use of deception in research continues to be debated, and its use is restricted by Institutional Review Boards (Sommers and Miller, 2013; Alberti and Güth, 2013; Krawczyk, 2015). Most laboratory measures of behavioral aggression, including the PSAP, typically involve the deception of an opponent who is either fictitious or a confederate. We try to increase the believability of the opponent by having the experimenter leave the participant at intervals to "go check on the other participant" and, more recently, by limiting the length of the game to ≤10 min. Often, the experimenter is testing several participants at the same time, which lends to the deception. When testing several participants at once, however, every attempt is made for some distance between the test rooms to limit the possibility of contact between participants. We have gauged participants' suspicion of whether their opponent was "real" (another participant) or "fictitious" (the computer program) by having participants describe their impressions of the opponent at the end of the study and by probing participants during debriefing. Examples of statements expressing suspicion are: "I was not sure if my competitor was stealing the points or if the computer was"; "Negative impression obviously, starting to think there is no other player...". In contrast, the majority of the statements suggested that participants thought the opponent was another participant: "he stole my points so we became enemies. I began to enjoy stealing his points. I hated him because he was a dick."; "I thought my competitor played the game as they were told to, just as I did. I believe he followed the instructions given and stuck to them"; "They liked to attack at the worse times. They might have waited till I didn't attack for a while."; "My opponent had a negative attitude because instead of earning he was trying to steal"; "I formed a negative impression- the competitor would steal my points and I would get irritated"; "I didn't really think about my competitor, just my points. But every time they stole points I stole theirs. Payback lol".

In the most common version of the PSAP that we have used (in which participants do not get to keep the points they steal), about 5–10% of participants express some suspicion regarding the PSAP and/or their opponent during debriefing. Nevertheless, in our studies, suspicion did not seem to be an important factor in the results; results remained the same when suspicious participants were excluded (e.g., Geniole et al., 2011). Further, when participants are explicitly told that their opponent will be the computer program, their aggressive responses are significantly lower than those of deceived participants (unpublished data). Therefore, suspicion of deception does not seem to be an important factor in the results, but explicitly informing participants that they are playing against a computer does affect the likelihood of an aggressive response.

Scoring aggressive behavior in the PSAP

Across studies, multiple methods for scoring PSAP aggression have been used. For example, the total number of steal presses (e.g., McCloskey et al., 2005; Moe et al., 2004; New et al., 2009), the number of steals relative to provocations (e.g., Cherek et al., 1997, 2000; Coccaro et al., 1996), the number of steals relative to earn presses (e.g., Gowin et al., 2010), and the number of steals relative to total presses (percentage of steals, e.g., Cote et al., 2013) were used. We also have used linear regression to isolate variability in aggressive responses by controlling statistically for earn and protect presses (e.g., Carré and McCormick, 2008). To prevent an artificial ceiling in button presses, in our more recent studies we changed the PSAP to allow a greater speed of button presses than permitted in the standard design; thus we use the percentage of steal presses before (proactive) and after (reactive) provocation to control for variability in speed. Although so many measurement options increases researcher degrees of freedom (Simmons et al., 2011), we have not found marked differences in the results when different scoring methods are used (e.g., percentage of steal presses or steal presses controlling for earn and protective presses), often obtaining high correlations between the various measurement methods (e.g., $rs > 0.86$ for correlations between the raw steal presses, the steal presses statistically controlling for earn and protect presses, and the percentage of steal presses relative to total presses; reanalysis of Geniole et al., 2013, $n = 201$).

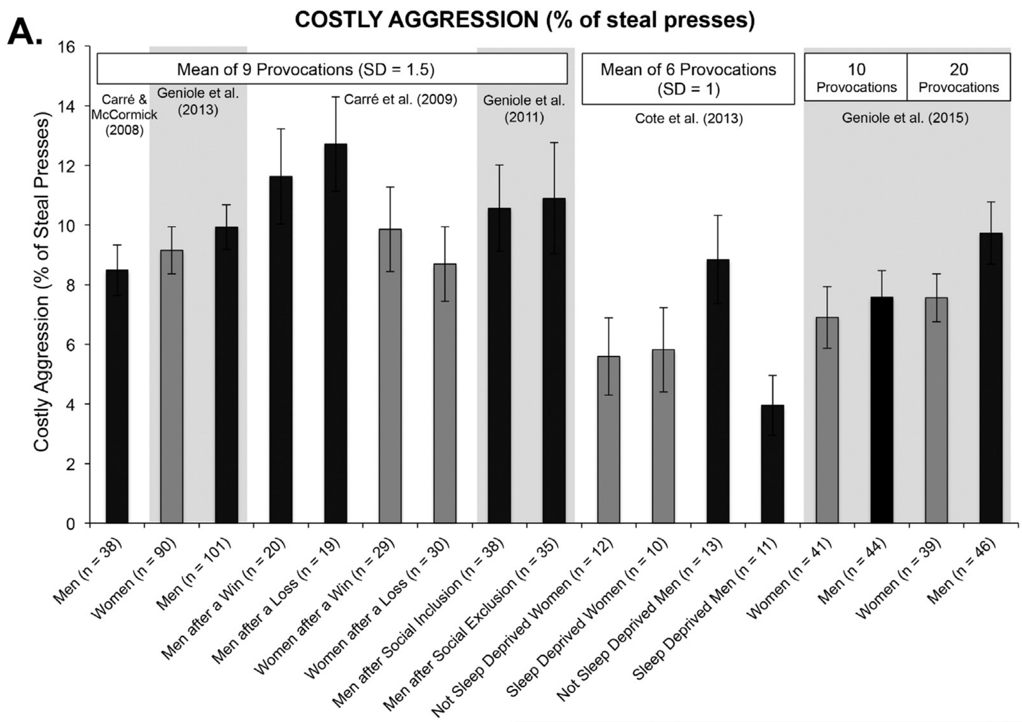
Comparing PSAP behavior across studies

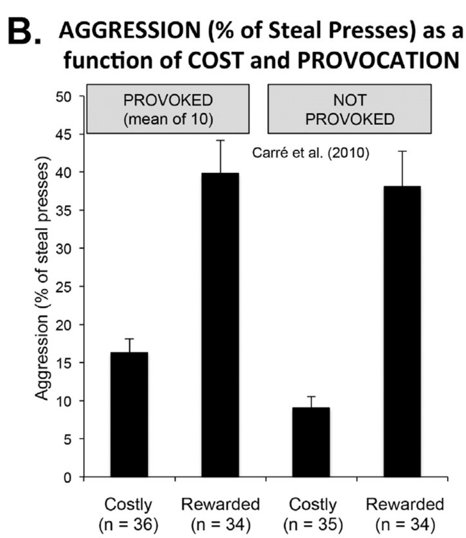
To allow comparison across our studies, we have re-scored the reactive aggression measure from each study as percentage of steal presses relative to total presses to illustrate how the experimental design and modifications to the PSAP affect this behavior (see Fig. 1). Panel A suggests that retaliation in the PSAP is increased in men in studies when a competitive event (either the Number Tracing Task, as in Carré et al., 2009; or Cyberball, as in Geniole et al., 2011) precedes the PSAP compared with in other studies. This finding is consistent with video game literature showing that competitive games increase aggressiveness in subsequent tasks (e.g., Adachi and Willoughby, 2011). Panel B shows how steal presses are increased when there is provocation compared with when there is not, and that steal presses are greatest when participants can keep points stolen, indicating that there is awareness of the tangible costs associated with steal presses that cannot be kept. Aggressive behavior in the PSAP is thus driven, in part, by cost-benefit analysis, consistent with findings from other studies, which reveal links between participants' appraisals of the costs and benefits associated with aggressive behaviors and their willingness and/or actual display of these behaviors (Archer and Southall, 2009; Archer et al., 2010; Rutter and Hine, 2005). Panel C outlines the procedural differences across the studies in Fig. 1.

Investigations of neuroendocrine function and the PSAP

Testosterone

Testosterone is perhaps the most widely investigated hormone in studies of competition and aggression. Although testosterone has been validated psychometrically as a biological individual difference variable (Sellers et al., 2007), baseline or trait levels of testosterone often share weak and inconsistent relationships with aggressive behavior (see meta-analysis in Archer et al., 2005). A similar trend emerges when





C.

Study	Number of Button Presses Required for each Option: Earn	Steal	Protect	Minimum Button Press Interval[a]	Duration of Round (min)	Mean (*SD*) steals per round
Carré and McCormick (2008)	100	10	10	170 ms	12	22.9 (16.6)
Carré et al. (2009)	100	10	10	170 ms	12	24.6 (15.1)
Carré et al. (2010)	50	50	50	170 ms	10	P-C: 7.4 (5.8); P-R: 22.3 (13.4); NP-R: 19.3 (14.5); NP-C: 3.1 (3.2)
Geniole et al. (2011)	50	10	10	170 ms	10	20.4 (16.0)
Cote et al. (2013)	100	10	10	50 ms	10	24.1 (21.8)
Geniole et al. (2013)	100	10	10	50 ms	10	40.1 (32.3)
Geniole et al. (2015)	100	10	10	50 ms	10	Study 1: 31.4 (26.7); Study 2: 30.2 (21.3)

Notes. [a]The minimum amount of time that must elapse between each button press. P = provoked. NP = not provoked. C = costly aggression. R = rewarded aggression.

Fig. 1. Aggression [percentage of steal presses relative to total button presses: steal presses / (earn presses + steal presses + protect presses)] across different types of PSAP rounds in studies from our lab. A. Studies in which steal presses were made with no financial gain to the participant (costly aggression). B. Study illustrating steal presses when they were costly versus rewarded (i.e., when participants did vs did not get to keep the points they stole), and when participants were provoked or not provoked during the round. C. Variations in PSAP parameters from study to study. Because provocation schedules were semi-random across participants, except for in Geniole et al., 2015, the mean number of provocations varied from study to study.

Table 2
Studies investigating neuroendocrine measures and aggression in the PSAP.

Experimental groups	*N*	Time of hormone measures	Pre-PSAP hormone & PSAP aggression	Change in hormone & PSAP aggression	Change in hormone during PSAP	Reference
Testosterone: Men						
Placebo vs testosterone cypionate (within-subject)	27			↑		Pope et al. (2000)[b]
No experimental groups	38	During: pre- and 10-min post-PSAP	*ns*	↑	↑	Carré and McCormick (2008)
Combined winners & losers of a fixed competition (Number Tracing Task)		Pre-PSAP, 10 min after competition.	*ns*	↑	↓	Carré et al. (2009)
(1) Losers	13		*ns*	↑		
(2) Winners	14		*ns*	*ns* (↑ when high in trait dominance)		
4 PSAP groups						
(1) Provoked & not rewarded for aggression	36	Before, during, and after PSAP rounds.	*ns*	Pre- to mid-PSAP: ↑ Pre- to post-PSAP: *ns*	*ns*	Carré et al. (2010)
(2) Not provoked & not rewarded	35		*ns*	Pre- to mid-PSAP: *ns* Pre- to post-PSAP: *ns*	*ns*	
(3) Provoked & rewarded	34		*ns*	Pre- to mid-PSAP: *ns* Pre- to post-PSAP: *ns*	*ns*	
(4) Not provoked & rewarded	34		*ns*	Pre- to mid-PSAP: *ns* Pre- to post-PSAP: *ns*	↑	
Combined those included in a Cyberball game and those excluded in a Cyberball game.		Pre-Cyberball to mid-PSAP	*ns*	↑	*ns*	Geniole et al. (2011)
(1) Socially included	33		*ns*	↑		
(2) Socially excluded	30		*ns*	*ns*		
Combined winners & losers of a competitive fighting video game	114	Pre-PSAP (before and after competition immediately before the PSAP)	*ns*	↑		Carré et al. (2013)
2 groups						
(1) Sleep deprived	9	Before and after PSAP.		*ns*	*ns*	Cote et al. (2013)
(2) Not sleep deprived	12			↑	*ns*	
No experimental groups	104	Before and after PSAP.	*ns*			Geniole et al. (2013)
No experimental groups	42	Before, during, and after PSAP.		*ns*	↑	Carré et al. (2014a)
Combined those in intervention and those in control schools		Before, during, and after PSAP.		↑	*ns*	Carré et al. (2014b)
(1) Intervention schools	34				*ns*	
(2) Control schools	29				*ns*	
2 studies						
(1) Continuum of low and high anxiety combined; all played fighting video game	106	Pre-PSAP (before and after video game)		Total sample: ↑ High anxious men: *ns* Low anxious men: ↑		Norman et al. (2014)
(2) Continuum of low and high anxiety combined; all played fighting video game	78	Pre-PSAP (before and after video game)		Total sample: *ns* High anxious men: *ns* Low anxious men: *ns*		
All participants combined	94	Pre-PSAP (two samples)	*ns*	*ns*		van Anders et al. (2014)
Testosterone: Women						
Low ($n = 6$) and high ($n = 5$) menstrual distress groups tested in phases of the menstrual cycle	11	Post-PSAP				Dougherty et al. (1997)
(1) Menses			*ns*			
(2) Midfollicular			↑			
(3) Ovulatory			*ns*			
(4) Pre-menses			*ns*			
Combined winners & losers of a fixed competition (Number Tracing Task)	60	Pre-PSAP, 10 min after competition.	*ns*	*ns*	↓	Carré et al. (2009)
No experimental groups	97	Before and after PSAP.	*ns*			Geniole et al. (2013)
Combined winners & losers of a competitive fighting video game	123	Pre-PSAP (before and after competition immediately before the PSAP)	*ns*	*ns*		Carré et al. (2013)
No experimental groups	41	Before, during, and after PSAP rounds.		*ns*	*ns*	Carré et al. (2014a)
Continuum of low and high anxiety combined; all played fighting video game	118	Pre-PSAP (before and after video game)		*ns*		Norman et al. (2014)
Cortisol: Men						
2 groups						
(1) Heroin addicts	20	Before and after PSAP	*ns*[a]		*ns*	Gerra et al. (2001)
(2) Controls	20		*ns*[a]		↑	
2 groups						
(1) Heroin addicts	20	Before and after PSAP	*ns*[a]		*ns*	Gerra et al. (2004)
(2) Controls	20		↑[a]		↑	
Combined those included in a Cyberball game		Pre-Cyberball to mid-PSAP	*ns*	↑	↓	Geniole et al. (2011)

(continued on next page)

Table 2 (*continued*)

Experimental groups	*N*	Time of hormone measures	Pre-PSAP hormone & PSAP aggression	Change in hormone & PSAP aggression	Change in hormone during PSAP	Reference
and those excluded in a Cyberball game						
(1) Socially included	33		*ns*	*ns*		
(2) Socially excluded	30		*ns*	*ns*		
Control and sleep deprived combined	21	Before and after PSAP.		*ns*	*ns*	Cote et al. (2013)
No experimental groups	104	Before and after PSAP.	*ns*			Geniole et al. (2013)
Placebo vs cortisol (within-subject)	45[e]			*ns*[d]		Gowin et al. (2013)
Cortisol: Women						
No experimental groups	97	Before and after PSAP.	*ns*			Geniole et al. (2013)
Placebo vs cortisol (within-subject)	45[e]			*ns*[d]		Gowin et al. (2013)
ACTH: Men						
2 groups						
(1) Heroin addicts	20	Before and after PSAP	*ns*[a]		*ns*	Gerra et al. (2001)
(2) Controls	20		*ns*[a]		↑	
2 groups						
(1) Heroin addicts	20	Before and after PSAP	*ns*[a]		↑	Gerra et al. (2004)
(2) Controls	20		*ns*[a]		↑	
Estradiol: Men						
No experimental groups	104	Before and after PSAP.	*ns*			Geniole et al. (2013)
Estradiol: Women						
No experimental groups	97	Before and after PSAP.	*ns*[c]			Geniole et al. (2013)
Growth hormone: Men						
2 groups						
(1) Heroin addicts	20	Before and after PSAP	*ns*[a]		*ns*	Gerra et al. (2001)
(2) Controls	20		*ns*[a]		↑	
Norepinephrine: Men						
2 groups						
(1) Heroin addicts	20	Before and after PSAP	↑[a]		↑	Gerra et al. (2001)
(2) Controls	20		↑[a]		↑	
2 groups						
(1) Heroin addicts	20	Before and after PSAP	↑[a]		↑	Gerra et al. (2004)
(2) Controls	20		↑[a]		↑	
Epinephrine: Men						
2 groups						
(1) Heroin addicts	20	Before and after PSAP	↑[a]		↑	Gerra et al. (2001)
(2) Controls	20		↑[a]		↑	
2 groups						
(1) Heroin addicts	20	Before and after PSAP	↑[a]		↑	Gerra et al. (2004)
(2) Controls	20		↑[a]		↑	
Testosterone × cortisol: Men						
Combined those included in a Cyberball game and those excluded in a Cyberball game	63	Pre-Cyberball to mid-PSAP	*ns*			Geniole et al. (2011)

Notes. Except for correlations corresponding to the "non-provoked" conditions in the study by Carré et al. (2010), the PSAP aggression represents steal presses that occurred during PSAP rounds in which participants were provoked (or post-provocation steal presses minus pre-provocation steal presses, Cote et al., 2013). Therefore, these measures are of reactive aggression in the PSAP.

[a] These values correspond to the findings for an analysis of the total area under the curve for the hormone measures, which can be influenced by both baseline and change scores.

[b] Another study (Kouri et al., 1995) also examined the effects of testosterone administration on PSAP aggression, but involved a smaller subset of the participants from (Pope et al., 2000) and thus was not included in the table.

[c] Bivariate simple correlation, *ns*; a negative relationship was observed when controlling for several variables, including cortisol and testosterone.

[d] The researchers also reported a marginally significant correlation between PSAP aggression and HPA-axis reactivity, $r = -0.28$, $p < 0.10$. Calculated by a different score, representing the area under the curve for cortisol on the drug administration day minus the area under the curve on the placebo administration day.

[e] $N = 45$ includes both males and females.

reviewing studies that have examined baseline testosterone and aggression in the PSAP, specifically (see Table 2). For example, of the 14 samples of male participants in which baseline testosterone and PSAP aggression was investigated, none of the associations were significant. Among samples of female participants, only one of the seven was significant; this positive relationship was found among women in the mid-follicular phase of their menstrual cycle but not during the ovulatory, pre-menses, and menses phases (Dougherty et al., 1997). Thus, there is no evidence in men and little evidence in women that baseline testosterone functions to influence aggressive behavior in the PSAP.

Rather than being stable, however, testosterone concentrations fluctuate throughout the day and in response to cues of competition and social instability (Archer, 2006; Wingfield et al., 1990). These fluctuations are considered functional in that they prepare the organism for antagonistic and competitive interactions over resources and mates (i.e., the Challenge Hypothesis, Wingfield et al., 1990; see also Mazur and Booth, 1998). As a consequence, individual differences in fluctuations in testosterone may be more relevant for modulating behavior than are baseline concentrations of this hormone (Carré et al., 2011). The studies in Table 2 provide limited evidence for an increase in testosterone during competition in the PSAP. Nevertheless, individual differences in the change in testosterone concentrations appear to be associated with aggression in the task. For example, greater increases (or lesser decreases) in testosterone were associated with greater aggressiveness in 12 different samples of men (see Table 2). There were also important moderators of this effect that might explain the non-significant associations in some studies. For example, testosterone changes shared stronger associations with PSAP aggression when participants were provoked and when aggression on the task was financially costly (vs not provoked or vs financially rewarding) (Carré et al., 2010), when they were well-rested (vs sleep deprived) (Cote et al., 2013), when they had just finished losing (vs winning) a preceding competitive interaction against the other PSAP player (Carré et al., 2009), and when they had been socially included (vs excluded) in a preceding computer task by the other PSAP player (Geniole et al., 2011). Also suggestive that any relationship may be situation-specific is that an increase in testosterone from hearing babies cry did not alter aggressive responding in the PSAP (van Anders et al., 2014). The associations were also moderated by individual difference factors: the relationship was stronger among men who were less (vs more) socially anxious (Norman et al., 2014) and, after a preceding victory, among men who were more (vs less) dominant (Carré et al., 2009). Therefore, moderators likely account for the heterogeneity in the effect across studies, with links between testosterone and PSAP aggression dependent on situational and individual difference factors; it is possible that these moderators may all tap into some common underlying motivational factor. Nevertheless, the reliability of these moderating factors is unknown in the absence of replication studies. There were no instances in which testosterone fluctuations shared a significant negative association with PSAP aggression; therefore, despite variation in the significance of the effect, the association between testosterone fluctuations and PSAP aggression appears directionally positive overall (although, it is possible that publication bias explains these directionally positive findings).

In Table 2, we have also indicated whether testosterone changes were measured before or during the PSAP for each sample. There is evidence of associations between testosterone changes and PSAP aggression in both instances, suggesting that these fluctuations are both associated with ongoing, and predict subsequent, aggressive behavior in the PSAP. Although the temporal separation between the change in testosterone and the aggressive behavior measured in the PSAP provides some support for the idea that testosterone surges cause increases in aggression in the task, it is also possible that a third variable (e.g., state anger) both promotes increases in testosterone and, subsequently, in aggressive behavior. To more definitively identify causal relationships, PSAP studies in which testosterone is experimentally manipulated are required. Researchers have begun using such approaches to identify causal relationships between testosterone and a variety of social behaviors (Boksem et al., 2013; Eisenegger et al., 2010; Mehta et al., 2015; van Honk et al., 2012; Wibral et al., 2012; for a review of administration studies, see Bos et al., 2012). One such study has been conducted with the PSAP (Pope et al., 2000; for a study involving a smaller subset of the same participants, see Kouri et al., 1995). The authors employed a randomized, double-blind, placebo-controlled study and found that testosterone administration increased aggressive responding in the PSAP relative to placebo. One limitation, however, is that the dose was supraphysiological and thus may not accurately characterize the relationship between testosterone and PSAP aggression when concentrations of the hormone surge within a normal physiological range. Future studies are thus required in which testosterone is manipulated within a normal physiological range in men (e.g., Eisenegger et al., 2013; Goetz et al., 2014).

Contrary to the reviewed literature for men, no studies to date have reported significant associations between changes in testosterone and PSAP aggression in women. Thus, links between testosterone fluctuations and PSAP aggression are likely sex-specific. Some researchers have suggested that the effects of testosterone on aggression are dependent on the hormone's conversion, through the enzyme aromatase, to estradiol (Trainor and Nelson, 2012). In one study (Geniole et al., 2013), we investigated this hormone in addition to testosterone; although neither hormone at baseline concentrations was associated with PSAP aggression in men in that particular study, a negative association between baseline estradiol and PSAP aggression emerged in women. This effect, however, was significant only after controlling statistically for the influence of testosterone, cortisol, hormonal contraceptive use, and personality traits (the bivariate relationship between estradiol and aggression was non-significant), highlighting the need for future research in this area. One possibility for the weaker associations in women is the greater measurement error because of the effects of menstrual cycle (e.g., Arslan et al., 2008) and hormonal contraceptives (e.g., Sowers et al., 2001) on hormone concentrations, as well as the lower concentrations of testosterone in women than in men.

Cortisol

Researchers have reported negative associations between baseline cortisol and aggression (reviewed in van Goozen et al., 2007) and costly punishment (e.g., Pfattheicher and Keller, 2014), positive associations between cortisol reactivity and aggression (e.g., Lopez-Duran et al., 2009), and some evidence that cortisol may moderate the link between testosterone and aggression (reviewed in Carré and Mehta, 2011). Nevertheless, many of these findings appear to be inconsistent across studies (e.g., baseline cortisol and cortisol reactivity: Alink et al., 2008; inconsistency in cortisol as a moderator: reviewed in Geniole et al., 2013). From the studies reviewed and summarized in Table 2, there is no evidence of an association between baseline cortisol and aggression in the PSAP, nor evidence of an interaction between cortisol and testosterone predicting aggression in the task (although there was only one test of the interaction and some research suggests this interaction may be further moderated by personality traits, Tackett et al., 2014, or that interactions between the changes in both of these hormones may be more important, Mehta et al., 2015). On the other hand, researchers have reported associations with PSAP aggression when cortisol was measured at two time points and the area under the curve (Gerra et al., 2004), cortisol reactivity (Geniole et al., 2011), or the effects of cortisol administration (e.g., Gowin et al., 2013) was analysed, rather than baseline cortisol. These associations were only found in samples that included men; there was only one test of the association between baseline cortisol and PSAP aggression in a sample involving only women, and it was non-significant. Thus, there appears to be some evidence for an association between cortisol and aggression in the PSAP in men but not women (except for in one mixed-sex sample, Gowin et al., 2013), and this relationship appears to emerge only when researchers examine naturally occurring or drug induced changes (or area under the curve) in this hormone.

In addition to cortisol, some researchers have examined adrenocorticotropic hormone (ACTH), which is responsible for stimulating the release of cortisol from the adrenal glands. Although concentrations of this hormone appear to increase during the PSAP (see Table 2), these increases (when measured as area under the curve) did not map onto PSAP aggression (Gerra et al., 2001, 2004).

Growth hormone, norepinephrine, and epinephrine

Gerra et al. (2001, 2004) have explored how concentrations of growth hormone, norepinephrine, and epinephrine, fluctuate during the PSAP and correlated with aggressive responding in the task among both heroin addicts and healthy volunteers. Norepinephrine and epinephrine showed consistent increases during the PSAP for both the healthy volunteers and the heroin addicts, whereas growth hormone only increased among healthy volunteers. Further, these increases of epinephrine and norepinephrine (as measured as area under the curve) were correlated positively with aggressive behavior in the task. Conversely, increases in growth hormone did not map onto aggressive behavior in the PSAP.

Predictive value of neuroendocrine function during PSAP

The PSAP has been used to examine how these neuroendocrine changes predict behavior measured in subsequent tasks. Specifically,

Please cite this article as: Geniole, S.N., et al., The Point Subtraction Aggression Paradigm as a laboratory tool for investigating the neuroendocrinology of aggression and competit..., Horm. Behav. (2016), http://dx.doi.org/10.1016/j.yhbeh.2016.04.006

we have found that testosterone fluctuations during the PSAP predicted subsequent antagonistic behavior towards the PSAP partner; men who showed greater increases in testosterone during the PSAP were more likely to give the other PSAP player a lower honorarium after the study than were participants who showed lesser increases (Geniole et al., 2013). In an earlier study, men who showed greater increases in testosterone during the PSAP were more likely to compete against the other PSAP player in a subsequent task than were men who showed lesser increases (Carré and McCormick, 2008). These PSAP-induced fluctuations in testosterone also appear to influence participants' perceptions of others: Men (but not women) who experienced greater increases in testosterone during the task judged faces posed in neutral expressions as less trustworthy than men who experienced lesser increases in testosterone during the task (Carré et al., 2014a). Thus, the PSAP also appears well-suited for inducing variability in testosterone fluctuations. This variability, in turn, may predict subsequent behavior and perceptions in men.

Conclusions

In sum, the PSAP is a measure of costly reactive aggression that lends itself well to investigations in a laboratory setting. An important advantage of the PSAP is that modifications can easily be introduced to the PSAP to accommodate a broad array of experimental questions and designs, particularly if using a program like E-PRIME® (https://www.pstnet.com/eprime.cfm) to generate the PSAP. For example, we currently are piloting a modified, dynamic version of the PSAP with E-PRIME® software in which participants actually compete against another participant. The software Inquisit by the company millisecond software (http://www.millisecond.com) also has a script of the version of the PSAP originally designed by Cherek et al. (1997), but we have no knowledge of the extent to which this version is modifiable. For researchers who have E-PRIME® software and would like to evaluate or use the PSAP in their own labs, we have included two of our E-PRIME versions of the PSAP (as used in Geniole et al., 2013 and Geniole et al., 2015) in the supplementary materials.

The PSAP has proved to be a useful tool for investigating individual differences in aggressive behavior during competition and the situational factors that promote aggression. Although the relationship between PSAP aggression and testosterone fluctuations are small and limited to men, the effects show some consistency across studies. There is evidence in species that neural sensitivity to testosterone is a better predictor of aggressive behavior than are testosterone concentrations in circulation (Rosvall et al., 2012). Although determination of androgen-induced gene expression in specific neural regions is not possible in human studies, another approach would be to consider variation in efficiency of androgen receptor signaling based on genotype (e.g., Raznahan et al., 2010; Manuck et al., 2010) as a factor in the relationship between testosterone and aggression. Positron emission tomography (PET) has been used to investigate neural regional differences in aromatase, the enzyme required for the conversion of testosterone to estradiol, in the human brain (Azcoitia et al., 2011), but this approach would not be practical or cost effective for the large sample studies required for investigation of individual differences in hormone and behavior relationships. Functional magnetic imaging of neural activations during PSAP play and their association with neuroendocrinological measures may also provide insight into individual variation in aggressive behavior.

Acknowledgements

The research described from our lab was supported by a Natural Sciences and Engineering Research Council (NSERC) Discovery Grant 288348 to CMM and a Social Sciences and Humanities Research Council (SSHRC) Canada Graduate Scholarship to SNG.

References

Adachi, P.J.C., Willoughby, T., 2011. The effect of video game competition and violence on aggressive behavior: which characteristic has the greatest influence? Psychol. Violence 1, 259–274.
Alberti, F., Güth, W., 2013. Studying deception without deceiving participants: an experiment of deception experiments. J. Econ. Behav. Organ. 93, 196–204.
Alink, L.R.A., van IJzendoorn, M.H., Bakermans-Kranenburg, M.J., Mesman, J., Juffer, F., Koot, H.M., 2008. Cortisol and externalizing behavior in children and adolescents: mixed meta-analytic evidence for the inverse relation of basal cortisol and cortisol reactivity with externalizing behavior. Dev. Psychobiol. 50, 427–450.
Allen, T.J., Dougherty, D.M., Rhoades, H.M., Cherek, D.R., 1996. A study of male and female aggressive responding under conditions providing an escape response. Psychol. Rec. 46, 651–664.
Anderson, C.A., Bushman, B.J., 2002. Human aggression. Psychology 53, 27–51.
Archer, J., 2006. Testosterone and human aggression: an evaluation of the challenge hypothesis. Neurosci. Biobehav. Rev. 30, 319–345.
Archer, J., Southall, N., 2009. Does cost–benefit analysis or self-control predict involvement in bullying behavior by male prisoners? Aggress. Behav. 35, 31–40.
Archer, J., Graham-Kevan, N., Davies, M., 2005. Testosterone and aggression: a reanalysis of Book, Starzyk, and Quinsey's (2001) study. Aggress. Violent Behav. 10, 241–261.
Archer, J., Fernández-Fuertes, A.A., Thanzami, V.L., 2010. Does cost–benefit analysis or self-control predict involvement in two forms of aggression? Aggress. Behav. 36, 292–304.
Arslan, A.A., Gu, Y., Zeleniuch-Jacquotte, A., Koenig, K.L., Liu, M., Velikokhatnaya, L., Shore, R.E., Toniolo, P., Linkov, F., Lokshin, A.E., 2008. Reproducibility of serum pituitary hormones in women. Cancer Epidemiol. Biomark. Prev. 17, 1880–1883.
Azcoitia, I., Yague, J.G., Garcia-Segura, L.M., 2011. Estradiol synthesis within the human brain. Neuroscience 191, 139–147.
Bailly, M.D., King, A.R., 2006. Trait modulation of alcohol-induced laboratory aggression. Psychiatry Res. 142, 129–138.
Baron, R.A., Richardson, D.R., 1994. Human Aggression. second ed. Plenum, New York.
Berkowitz, L., 1993. Aggression: Its Causes, Consequences, and Control. Temple University Press, NY, New York.
Boksem, M.A.S., Mehta, P.H., Van den Bergh, B., van Son, V., Trautmann, S.T., Roelofs, K., Smidts, A., Sanfey, A.G., 2013. Testosterone inhibits trust but promotes reciprocity. Psychol. Sci. 24, 2306–2314.
Bos, P.A., Panksepp, J., Bluthé, R.-M., van Honk, J., 2012. Acute effects of steroid hormones and neuropeptides on human social–emotional behavior: a review of single administration studies. Front. Neuroendocrinol. 33, 17–35.
Brown, G.L., Goodwin, F.K., Ballenger, J.C., Goyer, P.F., Major, L.F., 1979. Aggression in humans correlates with cerebrospinal fluid amine metabolites. Psychiatry Res. 1, 131–139.
Bubenzer-Busch, S., Herpertz-Dahlmann, B., Kuzmanovic, B., Gaber, T.J., Helmbold, K., Ullisch, M.G., Baurmann, D., Eickhoff, S.B., Fink, G.R., Zepf, F.D., 2015. Neural correlates of reactive aggression in children with attention-deficit/hyperactivity disorder and comorbid disruptive behaviour disorders. Acta Psychiatr. Scand. http://dx.doi.org/10.1111/acps.12475 (Epub ahead of print).
Buss, A.H., 1961. The Psychology of Aggression. Wiley and Sons, Hoboken, New Jersey.
Buss, A.H., Durkee, A., 1957. An inventory for assessing different kinds of hostility. J. Consult. Psychol. 21, 343.
Buss, A.H., Perry, M., 1992. The aggression questionnaire. J. Pers. Soc. Psychol. 63, 452–459.
Campbell, A., 1999. Staying alive: evolution, culture, and women's intrasexual aggression. Behav. Brain Sci. 22, 203–214.
Carré, J.M., McCormick, C.M., 2008. Aggressive behavior and change in salivary testosterone concentrations predict willingness to engage in a competitive task. Horm. Behav. 54, 403–409.
Carré, J.M., Mehta, P.H., 2011. Importance of considering testosterone–cortisol interactions in predicting human aggression and dominance. Aggress. Behav. 37, 489–491.
Carré, J.M., Putnam, S.K., McCormick, C.M., 2009. Testosterone responses to competition predict future aggressive behaviour at a cost to reward in men. Psychoneuroendocrinology 34, 561–570.
Carré, J.M., Gilchrist, J.D., Morrissey, M.D., McCormick, C.M., 2010. Motivational and situational factors and the relationship between testosterone dynamics and human aggression during competition. Biol. Psychol. 84, 346–353.
Carré, J.M., McCormick, C.M., Hariri, A., 2011. The social neuroendocrinology of human aggression. Psychoneuroendocrinology 36, 935–944.
Carré, J.M., Campbell, J.A., Lozoya, E., Goetz, S.M.M., Welker, K.M., 2013. Changes in testosterone mediate the effect of winning on subsequent aggressive behaviour. Psychoneuroendocrinology 38, 2034–2041.
Carré, J.M., Baird-Rowe, C.D., Hariri, A.R., 2014a. Testosterone responses to competition predict decreased trust ratings of emotionally neutral faces. Psychoneuroendocrinology 49, 79–83.
Carré, J.M., Iselin, A.-M.R., Welker, K.M., Hariri, A.R., Dodge, K.A., 2014b. Testosterone reactivity to provocation mediates the effect of early intervention on aggressive behavior. Psychol. Sci. 25, 1140–1146.
Cherek, D.R., 1981. Effects of smoking different doses of nicotine on human aggressive behavior. Psychopharmacology 75, 339–345.
Cherek, D.R., Schnapp, W., Moeller, F.G., Dougherty, D.M., 1996. Laboratory measures of aggressive responding in male parolees with violent and nonviolent histories. Aggress. Behav. 22, 27–36.
Cherek, D.R., Moeller, F.G., Dougherty, D.M., Rhoades, H., 1997. Studies of violent and nonviolent male parolees: II. Laboratory and psychometric measurements of impulsivity. Biol. Psychiatry 41, 523–529.
Cherek, D.R., Lane, S.D., Dougherty, D.M., Moeller, F.G., White, S., 2000. Laboratory and questionnaire measures of aggression among female parolees with violent or nonviolent histories. Aggress. Behav. 26, 291–307.

Cherek, D.R., Lane, S.D., Pietras, C.J., 2003. Laboratory measures: point subtraction aggression paradigm. Med. Psychiat. 22, 215–228.
Cima, M., Raine, A., 2009. Distinct characteristics of psychopathy relate to different subtypes of aggression. Personal. Individ. Differ. 47, 835–840.
Coccaro, E.F., Berman, M.E., Kavoussi, R.J., Hauger, R.L., 1996. Relationship of prolactin response to D-fenfluramine to behavioral and questionnaire assessments of aggression in personality-disordered men. Biol. Psychiatry 40, 157–164.
Coccaro, E.F., Berman, M.E., Kavoussi, R.J., 1997. Assessment of life history of aggression: development and psychometric characteristics. Psychiatry Res. 73, 147–157.
Cote, K.A., McCormick, C.M., Geniole, S.N., Renn, R.P., MacAulay, S.D., 2013. Sleep deprivation lowers reactive aggression and testosterone in men. Biol. Psychol. 92, 249–256.
Crockett, M.J., Apergis-Schoute, A., Herrmann, B., Lieberman, M.D., Müller, U., Robbins, T.W., Clark, L., 2013. Serotonin modulates striatal responses to fairness and retaliation in humans. J. Neurosci. 33, 3505–3513.
Daly, M., Wilson, M., 1988. Homicide. Transaction Publishers, New Brunswick, New Jersey.
De Quervain, D.J.F., Fischbacher, U., Treyer, V., Schellhammer, M., 2004. The neural basis of altruistic punishment. Science 305, 1254.
DeWall, C.N., Finkel, E.J., Lambert, N.M., Slotter, E.B., Bodenhausen, G.V., Pond, R.S., Renzetti, C.M., Fincham, F.D., 2013. The voodoo doll task: introducing and validating a novel method for studying aggressive inclinations. Aggress. Behav. 39, 419–439.
Dodge, K.A., Coie, J.D., 1987. Social-information-processing factors in reactive and proactive aggression in children's peer groups. J. Pers. Soc. Psychol. 53, 1146.
Dougherty, D.M., Bjork, J.M., Moeller, F.G., Swann, A.C., 1997. The influence of menstrual-cycle phase on the relationship between testosterone and aggression. Physiol. Behav. 62, 431–435.
Dougherty, D.M., Bjork, J.M., Huckabee, H.C.G., Moeller, F.G., Swann, A.C., 1999. Laboratory measures of aggression and impulsivity in women with borderline personality disorder. Psychiatry Res. 85, 315–326.
Eisenegger, C., Naef, M., Snozzi, R., Heinrichs, M., Fehr, E., 2010. Prejudice and truth about the effect of testosterone on human bargaining behaviour. Nature 463, 356–359.
Eisenegger, C., von Eckardstein, A., Fehr, E., von Eckardstein, S., 2013. Pharmacokinetics of testosterone and estradiol gel preparations in healthy young men. Psychoneuroendocrinology 38, 171–178.
Faris, R., Felmlee, D., 2011. Status struggles network centrality and gender segregation in same-and cross-gender aggression. Am. Sociol. Rev. 76, 48–73.
Friedman, A.F., Lewak, R., Webb, J.T., 1989. Psychological Assessment with the MMPI. Lawrence Erlbaum Associates, Hillsdale, NJ.
Gabay, A.S., Radua, J., Kempton, M.J., Mehta, M.A., 2014. The ultimatum game and the brain: a meta-analysis of neuroimaging studies. Neurosci. Biobehav. Rev. 47, 549–558.
Gallardo-Pujol, D., Andrés-Pueyo, A., Maydeu-Olivares, A., 2013. MAOA genotype, social exclusion and aggression: an experimental test of a gene–environment interaction. Genes Brain Behav. 12, 140–145.
Geniole, S.N., Carré, J.M., McCormick, C.M., 2011. State, not trait, neuroendocrine function predicts costly reactive aggression in men after social exclusion and inclusion. Biol. Psychol. 87, 137–145.
Geniole, S.N., Busseri, M.A., McCormick, C.M., 2013. Testosterone dynamics and psychopathic personality traits independently predict antagonistic behavior towards the perceived loser of a competitive interaction. Horm. Behav. 64, 790–798.
Geniole, S.N., Cunningham, C.E., Keyes, A.E., Busseri, M.A., McCormick, C.M., 2015. Costly retaliation is promoted by threats to resources in women and threats to status in men. Aggress. Behav. 41, 515–525.
Georgiev, A.V., Klimczuk, A.C.E., Traficonte, D.M., Maestripieri, D., 2013. When violence pays: a cost-benefit analysis of aggressive behavior in animals and humans. Evol. Psychol. 11, 678–699.
Gerra, G., Zaimovic, A., Raggi, M.A., Giusti, F., Delsignore, R., Bertacca, S., Brambilla, F., 2001. Aggressive responding of male heroin addicts under methadone treatment: psychometric and neuroendocrine correlates. Drug Alcohol Depend. 65, 85–95.
Gerra, G., Zaimovic, A., Moi, G., Bussandri, M., Bubici, C., Mossini, M., Raggi, M.A., Brambilla, F., 2004. Aggressive responding in abstinent heroin addicts: neuroendocrine and personality correlates. Prog. Neuro-Psychopharmacol. Biol. Psychiatry 28, 129–139.
Gerra, G., Zaimovic, A., Raggi, M.A., Moi, G., Branchi, B., Moroni, M., Brambilla, F., 2007. Experimentally induced aggressiveness in heroin-dependent patients treated with buprenorphine: comparison of patients receiving methadone and healthy subjects. Psychiatry Res. 149, 201–213.
Giancola, P.R., Parrott, D.J., 2008. Further evidence for the validity of the Taylor aggression paradigm. Aggress. Behav. 34, 214–229.
Gleason, E.D., Fuxjager, M.J., Oyegbile, T.O., Marler, C.A., 2009. Testosterone release and social context: when it occurs and why. Front. Neuroendocrinol. 30, 460–469.
Goetz, S.M.M., Tang, L., Thomason, M.E., Diamond, M.P., Hariri, A.R., Carré, J.M., 2014. Testosterone rapidly increases neural reactivity to threat in healthy men: a novel two-step pharmacological challenge paradigm. Biol. Psychiatry 76, 324–331.
Goldberg, L.R., Johnson, J.A., Eber, H.W., Hogan, R., Ashton, M.C., Cloninger, C.R., Gough, H.G., 2006. The international personality item pool and the future of public-domain personality measures. J. Res. Pers. 40, 84–96.
Golomb, B.A., Cortez-Perez, M., Jaworski, B.A., Mednick, S., Dimsdale, J., 2007. Point Subtraction Aggression Paradigm: validity of a brief schedule of use. Violence Vict. 22, 95–103.
Gowin, J.L., Swann, A.C., Moeller, F.G., Lane, S.D., 2010. Zolmitriptan and human aggression: interaction with alcohol. Psychopharmacology 210, 521–531.
Gowin, J.L., Green, C.E., Alcorn III, J.L., Swann, A.C., Moeller, F.G., Lane, S.D., 2013. The role of cortisol and psychopathy in the cycle of violence. Psychopharmacology 227, 661–672.
Granger, D.A., Shirtcliff, E.A., Booth, A., Kivlighan, K.T., Schwartz, E.B., 2004. The "trouble" with salivary testosterone. Psychoneuroendocrinology 29, 1229–1240.
Griskevicius, V., Tybur, J.M., Gangestad, S.W., Perea, E.F., Shapiro, J.R., Kenrick, D.T., 2009. Aggress to impress: hostility as an evolved context-dependent strategy. J. Pers. Soc. Psychol. 96, 980–994.
Güth, W., Schmittberger, R., Schwarze, B., 1982. An experimental analysis of ultimatum bargaining. J. Econ. Behav. Organ. 3, 367–388.
Hawley, P.H., 2007. Social dominance in childhood and adolescence: why social competence and aggression may go hand in hand. In: Hawley, P.H., Little, T.D., Rodkin, P.C. (Eds.), Aggression and Adaptation: The Bright Side to Bad Behavior. Lawrence Erlbaum Associates, Hillsdale NJ, pp. 1–29.
Hawley, P.H., Vaughn, B.E., 2003. Aggression and adaptive functioning: the bright side to bad behavior. Merrill-Palmer Q. 49, 239–242.
Herr, N.R., Jones, A.C., Cohn, D.M., Weber, D.M., 2015. The impact of validation and invalidation on aggression in individuals with emotion regulation difficulties. Personal. Disord. Theory, Res. Treat. 6, 310–314.
Kose, S., Steinberg, J.L., Moeller, F.G., Gowin, J.L., Zuniga, E., Kamdar, Z.N., Schmitz, J.M., Lane, S.D., 2015. Neural correlates of impulsive aggressive behavior in subjects with a history of alcohol dependence. Behav. Neurosci. 129, 183–196.
Kouri, E.M., Lukas, S.E., Pope, H.G., Oliva, P.S., 1995. Increased aggressive responding in male volunteers following the administration of gradually increasing doses of testosterone cypionate. Drug Alcohol Depend. 40, 73–79.
Krawczyk, M., 2015. "Trust me, I am an economist." A note on suspiciousness in laboratory experiments. J. Behav. Exp. Econ. 55, 103–107.
Kuepper, Y., Grant, P., Wielpuetz, C., Hennig, J., 2013. MAOA-uVNTR genotype predicts interindividual differences in experimental aggressiveness as a function of the degree of provocation. Behav. Brain Res. 247, 73–78.
Lieberman, J.D., Solomon, S., Greenberg, J., McGregor, H.A., 1999. A hot new way to measure aggression: hot sauce allocation. Aggress. Behav. 25, 331–348.
Lieving, L.M., Cherek, D.R., Lane, S.D., Tcheremissine, O.V., Nouvion, S.O., 2008. Effects of acute tiagabine administration on aggressive responses of adult male parolees. J. Psychopharmacol. 22, 144–152.
Lopez-Duran, N.L., Olson, S.L., Hajal, N.J., Felt, B.T., Vazquez, D.M., 2009. Hypothalamic pituitary adrenal axis functioning in reactive and proactive aggression in children. J. Abnorm. Child Psychol. 37, 169–182.
Manuck, S.B., Marsland, A.L., Flory, J.D., Gorka, A., Ferrell, R.E., Hariri, A.R., 2010. Salivary testosterone and a trinucleotide (CAG) length polymorphism in the androgen receptor gene predict amygdala reactivity in men. Psychoneuroendocrinology 35, 94–104.
Marsh, D.M., Dougherty, D.M., Moeller, F.G., Swann, A.C., Spiga, R., 2002. Laboratory-measured aggressive behavior of women: acute tryptophan depletion and augmentation. Neuropsychopharmacology 26, 660–671.
Mazur, A., 2006. The role of testosterone in male dominance contests that turn violent. Soc. Biol. 53, 24–29.
Mazur, A., Booth, A., 1998. Testosterone and dominance in men. Behav. Brain Sci. 21, 353–363.
McCloskey, M.S., Berman, M.E., Coccaro, E.F., 2005. Providing an escape option reduces retaliatory aggression. Aggress. Behav. 31, 228–237.
McCloskey, M.S., New, A.S., Siever, L.J., Goodman, M., Koenigsberg, H.W., Flory, J.D., Coccaro, E.F., 2009. Evaluation of behavioral impulsivity and aggression tasks as endophenotypes for borderline personality disorder. J. Psychiatr. Res. 43, 1036–1048.
Mehta, P.H., van Son, V., Welker, K.M., Prasad, S., Sanfey, A.G., Smidts, A., Roelofs, K., 2015. Exogenous testosterone in women enhances and inhibits competitive decision-making depending on victory–defeat experience and trait dominance. Psychoneuroendocrinology 60, 224–236.
Moe, B.K., King, A.R., Bailly, M.D., 2004. Retrospective accounts of recurrent parental physical abuse as a predictor of adult laboratory-induced aggression. Aggress. Behav. 30, 217–228.
Moeller, F.G., Dougherty, D.M., Rustin, T., Swann, A.C., Allen, T.J., Shah, N., Cherek, D.R., 1997. Antisocial personality disorder and aggression in recently abstinent cocaine dependent subjects. Drug Alcohol Depend. 44, 175–182.
New, A.S., Hazlett, E.A., Newmark, R.E., Zhang, J., Triebwasser, J., Meyerson, D., Lazarus, S., Trisdorfer, R., Goldstein, K.E., Goodman, M., 2009. Laboratory induced aggression: a positron emission tomography study of aggressive individuals with borderline personality disorder. Biol. Psychiatry 66, 1107–1114.
Norman, R.E., Moreau, B.J.P., Welker, K.M., Carré, J.M., 2014. Trait anxiety moderates the relationship between testosterone responses to competition and aggressive behavior. Adapt. Hum. Behav. Physiol. 1, 312–324.
Pellegrini, A.D., 2007. Is aggression adaptative? Yes: some kinds are and in some ways. In: Hawley, P.H., Little, T.D., Rodkin, P.C. (Eds.), Aggression and Adaptation: The Bright Side to Bad Behavior. Lawrence Erlbaum Associates, Hillsdale NJ, pp. 85–105.
Pfattheicher, S., Keller, J., 2014. Towards a biopsychological understanding of costly punishment: the role of basal cortisol. PLoS ONE 9. http://dx.doi.org/10.1371/journal.pone.0085691.
Pinto, D.G., Maltby, J., Wood, A.M., Day, L., 2012. A behavioral test of Horney's linkage between authenticity and aggression: people living authentically are less-likely to respond aggressively in unfair situations. Personal. Individ. Differ. 52, 41–44.
Pope, H.G., Kouri, E.M., Hudson, J.I., 2000. Effects of supraphysiologic doses of testosterone on mood and aggression in normal men: a randomized controlled trial. Arch. Gen. Psychiatry 57, 133–140.
Raznahan, A., Lee, Y., Stidd, R., Long, R., Greenstein, D., Clasen, L., Addington, A., Gogtay, N., Rapoport, J.L., Giedd, J.N., 2010. Longitudinally mapping the influence of sex and androgen signaling on the dynamics of human cortical maturation in adolescence. Proc. Natl. Acad. Sci. 107, 16988–16993.
Rilling, J.K., Sanfey, A.G., 2011. The neuroscience of social decision-making. Annu. Rev. Psychol. 62, 23–48.
Rosvall, K.A., 2013. Proximate perspectives on the evolution of female aggression: good for the gander, good for the goose? Philos. Trans. R. Soc. B Biol. Sci. 368. http://dx.doi.org/10.1098/rstb.2013.0083.

Please cite this article as: Geniole, S.N., et al., The Point Subtraction Aggression Paradigm as a laboratory tool for investigating the neuroendocrinology of aggression and competit..., Horm. Behav. (2016), http://dx.doi.org/10.1016/j.yhbeh.2016.04.006

Rosvall, K.A., Burns, C.M.B., Barske, J., Goodson, J.L., Schlinger, B.A., Sengelaub, D.R., Ketterson, E.D., 2012. Neural sensitivity to sex steroids predicts individual differences in aggression: implications for behavioural evolution. Proc. R. Soc. Biol. Sci. 279, 3547–3555.

Rutter, A., Hine, D.W., 2005. Sex differences in workplace aggression: an investigation of moderation and mediation effects. Aggress. Behav. 31, 254–270.

Sanfey, A.G., Rilling, J.K., Aronson, J.A., Nystrom, L.E., Cohen, J.D., 2003. The neural basis of economic decision-making in the ultimatum game. Science 300, 1755–1758.

Schuster, I., 1983. Women's aggression: an African case study. Aggress. Behav. 9, 319–331.

Schlüter, T., Winz, O., Henkel, K., Eggermann, T., Mohammadkhani-Shali, S., Dietrich, C., Heinzel, A., Decker, M., Cumming, P., Zerres, K., 2016. MAOA-VNTR polymorphism modulates context-dependent dopamine release and aggressive behavior in males. NeuroImage 125, 378–385.

Sellers, J.G., Mehl, M.R., Josephs, R.A., 2007. Hormones and personality: testosterone as a marker of individual differences. J. Res. Pers. 41, 126–138.

Simmons, J.P., Nelson, L.D., Simonsohn, U., 2011. False-positive psychology undisclosed flexibility in data collection and analysis allows presenting anything as significant. Psychol. Sci. 22, 1359–1366.

Singer, T., Seymour, B., O'Doherty, J.P., Stephan, K.E., Dolan, R.J., Frith, C.D., 2006. Empathic neural responses are modulated by the perceived fairness of others. Nature 439, 466–469.

Skibsted, A.P., Da Cunha-Bang, S., Carré, J.M., Hansen, A.E., Beliveau, V., Knudsen, G.M., Fisher, P.M., 2015. Aggression-related brain function assessed with the point subtraction aggression paradigm in functional magnetic resonance imaging. Eur. Neuropsychopharmacol. 25, S191.

Soma, K.K., Rendon, N.M., Boonstra, R., Albers, H.E., Demas, G.E., 2015. DHEA effects on brain and behavior: insights from comparative studies of aggression. J. Steroid Biochem. Mol. Biol. 145, 261–272.

Sommers, R., Miller, F.G., 2013. Forgoing debriefing in deceptive research: is it ever ethical? Ethics Behav. 23, 98–116.

Sorgi, P., Ratey, J.J., Knoedler, D.W., Markert, R.J., Reichman, M., 1991. Rating aggression in the clinical setting: a retrospective adaptation of the Overt Aggression Scale: preliminary results. J. Neuropsychiatr. Clin. Neurosci. 3, s52–s56.

Sowers, M.F., Beebe, J.L., McConnell, D., Randolph, J., Jannausch, M., 2001. Testosterone concentrations in women aged 25–50 years: associations with lifestyle, body composition, and ovarian status. Am. J. Epidemiol. 153, 256–264.

Spielberger, C.D., Sydeman, S.J., 1994. State-Trait Anxiety Inventory and State-Trait Anger Expression Inventory. In: Maruish, M.E. (Ed.), The Use of Psychological Testing for Treatment Planning and Outcome Assessment, pp. 292–321 (Hillsdale, NJ).

Straus, M.A., 1979. Measuring intrafamily conflict and violence: the conflict tactics (CT) scales. J. Marriage Fam. 41, 75–88.

Sutton, J., Smith, P.K., Swettenham, J., 1999. Socially undesirable need not be incompetent: a response to Crick and Dodge. Soc. Dev. 8, 132–134.

Tackett, J.L., Herzhoff, K., Harden, K.P., Page-Gould, E., Josephs, R.A., 2014. Personality × hormone interactions in adolescent externalizing psychopathology. Personality Disord. 5, 235–246.

Taylor, S.P., 1967. Aggressive behavior and physiological arousal as a function of provocation and the tendency to inhibit aggression1. J. Pers. 35, 297–310.

Tcheremissine, O.V., Lane, S.D., Lieving, L.M., Rhoades, H.M., Nouvion, S., Cherek, D.R., 2005. Individual differences in aggressive responding to intravenous flumazenil administration in adult male parolees. J. Psychopharmacol. 19, 640–646.

Tedeschi, J.T., Quigley, B.M., 1996. Limitations of laboratory paradigms for studying aggression. Aggress. Violent Behav. 1, 163–177.

Trainor, B.C., Nelson, R.J., 2012. Neuroendocrinology of aggression. In: Fink, G., Pfaff, D.W., Levine, J. (Eds.), Handbook of Neuroendocrinology, pp. 509–520.

van Anders, S.M., Tolman, R.M., Jainagaraj, G., 2014. Examining how infant interactions influence men's hormones, affect, and aggression using the Michigan Infant Nurturance Simulation Paradigm. Fathering 12, 143–160.

van Goozen, S.H.M., Fairchild, G., Snoek, H., Harold, G.T., 2007. The evidence for a neurobiological model of childhood antisocial behavior. Psychol. Bull. 133, 149.

van Honk, J., Montoya, E.R., Bos, P.A., van Vugt, M., Terburg, D., 2012. New evidence on testosterone and cooperation. Nature 485, E4–E5.

Walls, S.C., Jaeger, R.G., 1987. Aggression and exploitation as mechanisms of competition in larval salamanders. Can. J. Zool. 65, 2938–2944.

White, S.F., Brislin, S.J., Sinclair, S., Blair, J.R., 2014. Punishing unfairness: rewarding or the organization of a reactively aggressive response? Hum. Brain Mapp. 35, 2137–2147.

Wibral, M., Dohmen, T., Klingmüller, D., Weber, B., Falk, A., 2012. Testosterone administration reduces lying in men. PLoS ONE 7, e46774.

Wingfield, J.C., Hegner, R.E., Dufty Jr., A.M., Ball, G.F., 1990. The "challenge hypothesis": theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. Am. Nat. 136, 829–846.

Yamagishi, T., Horita, Y., Takagishi, H., Shinada, M., Tanida, S., Cook, K.S., 2009. The private rejection of unfair offers and emotional commitment. Proc. Natl. Acad. Sci. 106, 11520–11523.

Yudofsky, S.C., Silver, J.M., Jackson, W., Endicott, J., Williams, D., 1986. The Overt Aggression Scale for the objective rating of verbal and physical aggression. Am. J. Psychiatry 143, 35–39.

Zhou, J., Wang, X., Li, L., Cao, X., Xu, L., Sun, Y., 2006. Plasma serotonin levels in young violent offenders: aggressive responding and personality correlates. Prog. Neuro-Psychopharmacol. Biol. Psychiatry 30, 1435–1441.

Please cite this article as: Geniole, S.N., et al., The Point Subtraction Aggression Paradigm as a laboratory tool for investigating the neuroendocrinology of aggression and competit..., Horm. Behav. (2016), http://dx.doi.org/10.1016/j.yhbeh.2016.04.006