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Are personality traits consistent in fish? − The influence of social context

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Abstract :

Individual differences in behavioural and physiological responses to challenges are progressively accepted as adaptive variation and reveal a strong degree of evolutionary conservation throughout the vertebrate taxa. Previous studies in gilthead seabream (*Sparus aurata*) suggested that individual differences in behaviour reflect distinct coping styles or personality, contrasting consistent traits associations. One of the traits that have been shown to be consistent over time and across context is the escape response under a restraining test. Using this trait as a proxy of personality in seabream the influence of social context in the consistency of escape behaviour was investigated. Individually tagged juvenile seabream ($n = 360$; 70.18 ± 11.44 g; mean ± SD) were subjected to a restraining test that consisted of keeping each fish in an emerged net for one minute. Behaviours measured in the net (latency to escape; number of escape attempts and total time spent on escaping) were collapsed into first principal component scores using Principal Components Analysis (PCA). Using the PCA scores the individuals were distributed into homogeneous groups ($n = 30$ each group) of proactive, reactive and intermediate. Control groups consisted of mixed groups with 1/3 of each coping style. After one month the same individuals were exposed to the same test (restraining test) to assess consistency of behavioural responses. Results indicate that homogenous groups of proactive ($p = 0.086$) and reactive ($p = 0.159$) individuals did not exhibit consistent behavioural responses as opposed to the intermediate ($p = 0.028$) and control groups ($p < 0.001$). This study thus confirms that the social context in which fish are kept significantly influence personality traits.

Highlights

► Escape responses from a net can be used as a proxy for personality in seabream. ► Grouping individuals with similar personality results in personality changes. ► Grouping individuals with different personality suggests consistent personality traits. ► Social context influences personality traits in gilthead seabream (*Sparus aurata*).

Keywords : Individual variation, *Sparus aurata*, Coping styles, Behavioural syndromes, Group composition, Social information

1. Introduction

In recent years the study of individual differences in behavioural and physiological responses to challenges (i.e. animal personality or coping style) has been increasing considerably. The adaptive importance of individual variability has become a central subject in a wide range of different biological disciplines ranging from behavioural ecology to biomedical research (Francis 1990; Gosling 2001; Koolhaas et al. 1999; Sih et al. 2004).

Despite the diversity of terminology and designated definitions (Francis 1990; Gosling 2001; Koolhaas et al. 1999; Sih et al. 2004), there seems to be a consensus that individual variation may be consistent and biologically meaningful, and individual differences in certain behavioural traits are consistent and predictive of other behaviours or physiological responses shown in another context (Koolhaas et al. 1999).

Several studies in fish have provided early documentation on individual consistency in behaviour (Brelin et al. 2005; Castanheira et al. 2013ab; Huntingford 1976; Martins et al. 2012; Millot et al. 2014; Øverli et al. 2004) that reflects distinct personality traits usually categorized in two contrasting personality types, proactive (active coping or bold or 'fight-flight') and reactive (passive coping or shy or 'non-aggressive' (Koolhaas et al. 1999; Øverli et al. 2007). Behaviourally, proactive individuals are characterised by active avoidance, low flexibility, high levels of aggression, territorial control, and other behavioural responses that suggest active efforts to counteract a negative stimulus, this pattern being the opposite for reactive individuals (Koolhaas et al. 1999 and 2010, Ruiz-Gomes et al. 2011).

Seabream (*Sparus aurata*) is one of the most important farmed species in the Mediterranean. Recently, the presence of personality types in seabream has been shown based on individual differences in cortisol responsiveness after a restraining test (Castanheira et al. 2013a), together with individual differences in behavioural responses to a variety of challenges that are consistent over time and across contexts using both individual and grouped-based tests (Castanheira et al. 2013b). Using the previous results we can hypothesize that some dimensions of personality, more specifically the escape response (avoidance) can be influenced by the group where the fish are reared. Avoidance is the tendency or absence of the tendency to engage with novelty, and is accepted as one of the main dimensions of personality in animals (Réale et al. 2007). The existence of individual variation in the escape response and the influence of social context on that response are likely to have an impact in adaptability and welfare in aquaculture rearing conditions. Despite the ecological significance (predator-prey-interaction) and physiological implications (anaerobic recovery capacity of white muscle) of the escape response in aquaculture rearing condition that trait can be easily accessed during normal rearing procedures (e.g. grading, vaccination, transport).

Indeed, it is well documented that social context exerts considerable influence on the individual personality (Webster and Ward 2011). Social processes, such as conformity (the tendency of individuals to adopt the behaviour of the majority of their group mates) and facilitation (the presence of group mates affects the behaviour of an individual, allowing individuals to perform behaviours that they would not do if they were alone) exert a known influence on the behaviour of grouping animals and hence isolated animals could behave differently (Magnhagen and Staffan 2005; Magnhagen 2007; Magnhagen and Bunnefeld 2009). The importance of social context in fish is also illustrated by its role in social familiarity (Galhardo et al. 2012), social dominance (Montero et al. 2009), social plasticity (Oliveira 2009, 2012) and social learning (Brown et al. 2003). Therefore, it is expected that personality traits are flexible when exposed to distinct environmental conditions (e.g. social group), dependent of the social relationship and personality of the individuals group members.

Thus, while the importance of sociability in personality is recognised, the study of social context in fish typically address the effect of group size or composition, and potential effects of social context (group composition) on stress response have been so far largely ignored.

With all this in mind, the present research investigates the effect of avoidance in gilthead seabream kept under different social contexts, i.e. the influence of other group members on an individual avoidance behaviour consistency.

2. Methods

The experiment described was conducted in accordance with the Guidelines of the European Union Council (86/609/EU) and Portuguese legislation for the use of laboratory animals, and approved by the ethics committee from the Veterinary Medicines Directorate, the Portuguese competent authority for the protection of animals, Ministry of Agriculture, Rural Development and Fisheries, Portugal. Permit number 0420/000/000-n.99-09/11/2009.

2.1. Experimental animals, housing and feeding

The experiment was carried out at the Ramalhete Research Station from CCMAR (Faro, Portugal). All animals used were randomly selected from a population, housed in two fibreglass stock tanks (500L) n=250 per tank under standard rearing conditions (Morales 1983). All animals were obtained from a seabream producer (MARESA Mariscos de Esteros SA, Huelva, Spain) and were kept in stock groups until the start of the experiment. Individuals were anaesthetised with 2-phenoxyethanol (0.5 ‰, Sigma-Aldrich) which rendered them completely motionless within 10 s of immersion and individually PIT-tagged (Trovan®, Netherlands) in the muscle under the dorsal fin. After tagging fish were placed in a bucket with clear water and aeration to recovery from the anaesthetic before laid in the rearing tanks. All the individuals were recovery within 30 s in maximum from the anaesthetic procedure. This procedure were done two weeks before the start of the experimental procedures. During rearing water temperature (22.3±1.2 ºC), salinity (35.9±1.4 ‰), dissolved oxygen (98.1±1.8 %), NO_2-N (0.0±0.0 mg L^{-1}) and NO_3-N (0.0±0.0 mg L^{-1}) were checked daily and a natural photoperiod was provided. Fish were fed 2% BW day^{-1} , by hand, twice per day (09:30 and

14:30), with a commercial diet (Aquagold 3mm, Sorgal SA, Portugal; 44 % crude protein, 14 % crude fat, 8 % ash, 2.5 % crude fibres, 1.0 % phosphorus). The same feed and photoperiod was used during all experimental procedures.

2.2. Experimental procedures

Individually tagged Seabream juveniles (n=360; 70.18 ± 11.44 g; mean ± SD) were subjected to a net restraining test for personality screening. The escape behaviour under a restraining test is one of the traits that have been shown to be consistent over time and across context in previous studies (Castanheira et al. 2013b). Briefly, the net restraining test consists of holding each fish individually in an emerged net for three minutes. While in the net the following behaviours were measured: i) latency to escape (time in seconds taken by each fish to show an escape attempt; escape attempt was defined as an elevation of the body from the net; ii) number of escape attempts and iii) total time spent on escape attempts (total time in seconds taken by each fish escaping since the first to the last escape attempts) (for details see Castanheira et al. 2013b). Behaviours measured in the net were video recorded, analysed and collapsed into first principal component scores using Principal Components Analysis (PCA) in order to obtain a score allowing the individual characterization of personality. Individuals presenting a high latency to escape, low number of escape attempts and shorter total time escaping were characterized by a low score and identified as reactive fish. Individuals presenting a lower latency to escape, high number of escape attempts and longer total time escaping were characterized by a high score and identified as proactive. These scores were used as a continuous variable with a range from -1.07 to 1.08. Using the PCA scores the individuals were distributed into homogeneous groups (n=30 each group; in triplicate) of proactive, reactive and intermediate. Control groups consisted of mixed groups with 1/3 of each coping style (10 proactive, 10 reactive and 10 intermediate animals). Experimental groups were kept in plastic tanks (100 L) during one month. After this period the same individuals were exposed to the same test (restraining test final) to assess the consistency of behavioural responses.

2.3. Data analysis

Statistical analyses were performed using SPSS 19.0 for Windows. The results are expressed as mean±standard deviation (SD). Behaviours measured in the net restraining test were collapsed into first principal component scores (PC1) with orthogonal rotation (varimax) using Principal Components Analysis (PCA). The correlation matrix was used to check multicollinearity, i.e., to identify variables that did not correlate with any other variable, or correlate very highly (r=0.9) with one or more other variables. Kaiser–Meyer–Olkin (KMO) test for sample adequacy was always greater than 0.5 and the Bartlett's test of sphericity was significant for all tests.
Spearman correlation analyses were used when data failed to pass the Kolmogorov-Smirnov test for normality. Statistical significance was taken at $p<0.05$.

3. Results

Table 1 depicts the pronounced individual variation during the restraining test: latency to escape, number of escape attempts and total time escaping. Individuals performed on average 10 escape movements for a total escape time of around 14 seconds and a latency to escape of 18 seconds. Latency to escape had the higher variation of the measured variables, with a range from 1 to 180 seconds.

The order of restraining was randomized and no effect of order was detected (p=0.615). In addition, no significant differences in body weight were observed between individuals with different coping styles (p=0.785).

The correlation between the personality scores (initial and final) to assess consistency of behavioural responses is shown in Figure 1. Personality scores were significantly correlated with final restraining scores in intermediate (r_s=0.290, p=0.028) and control groups (r_s=0.458, p<0.001). No correlation was found between the homogenous groups of proactive (r_s=0.209, p=0.086) and reactive (r_s=0.175, p=0.159) individuals, demonstrate that proactive and reactive individuals were more likely to re-adjust their individual escape behaviour as opposed to the intermediate and control individuals.

Some fish lost the PIT-tags during the experiment thus, it was not possible to analyse the behaviours of all individuals. However the sample size used was still very robust: (n=69 proactive, n=57 intermediate, n=66 reactive and n=79 control individuals.

The correlation between the escape behaviour during three minutes and the first minute of the restraining test is shown in Figure 2. The first minute of restraining scores was significantly correlated with the three minutes for the initial (r_s=0.680, p<0.001) and final (r_s=0.775, p<0.001) screening.

4. Discussion

The main objective of the current study was to investigate the consistency of escape behaviour; one of the main dimensions of personality in animals, in fish kept under different social contexts i.e. the influence of other group members on the consistency of individual avoidance behaviour. Here, the escape/avoidance response during the restraining test indicated a consistent personality trait in intermediate and control groups: individuals showing lower latency to escape, higher number of escape attempts and spending more time escaping during the initial screening, showed a similar behaviour after one month when the test was repeated. In proactive and reactive groups, no correlation was found.

Available evidence suggests that social context strongly influence the individual personality (Webster and Ward 2011). Social context is involved in the regulation of numerous characteristic behaviours such as social facilitation (Webster et al. 2007), social familiarity

(Galhardo et al. 2012), social dominance (Montero et al. 2009), social plasticity (Oliveira 2009,2012) and social learning (Brown et al. 2003). The presence of conspecifics may cause individuals to enhance or suppress threat-sensitive behaviour such as activity, exploration/risk, foraging, feeding rate and courting opportunities (Schuett et al. 2010,2011; Cote et al. 2010,2011). Furthermore, individuals with extreme personality types may be affected in a different way. We expected that reactive individuals are more sensitive to isolation and try to adjust/follow more often the behaviour of other group members than proactive individuals. In perch (*Perca fluviatilis*), a modulation of individual behaviours by other group members was suggested and bolder individuals changed the behaviour less when alone than shyer, and had a higher influence in the group. (Magnhagen and Staffan 2005; Magnhagen 2007; Magnhagen and Bunnefeld 2009) The same studies showed that even though the presence of conspecifics significantly affected individual behaviour compared to when alone, the individual behavioural responses remained predictable in isolation or under social contexts. Therefore, the degree of change induced by the presence of conspecifics on the individuals responses, compared to when alone, is also influenced by the initial responsiveness of the individual (Magnhagen and Staffan 2005; Magnhagen 2007; Magnhagen and Bunnefeld 2009).

Moreover, Webster et al. (2007) showed a link between boldness and social facilitation in three spine sticklebacks (*Gasterosteus aculeatus*). When bolder individuals (more active) were tested alone, those that were more active resumed foraging sooner when subjected to a simulated predator attack, and also consumed a higher number of preys in foraging competition trials. However, this relationship was not observed when additional conspecifics were present, demonstrating significant effects of group size upon boldness.

Our results therefore suggest the potential influence of the social context in fish. A finding that can be explained by the fact that individuals tending to adjust their social behaviour according to the available social information in the group, in order to adjust and optimize their own personality type. These adjustments could have an ecological and evolutionary significance related with adaptation to new environmental conditions. Social support might be an advantage to allow individuals to work in cooperation to enhance investment in more profitable activities such as foraging, exploration and mating. The heterogeneity in avoidance response of the group may support some individuals to flourish when the environment change. In addition, the understanding of those differences may have several practical implications. One example is the possibility to takes advantage of this social behaviour and develops rearing conditions accordingly. For example the aquaculture industry may takes advantage of this group heterogeneity in semi-intensive and extensive conditions where the individuals are more susceptible to environmental changes (i.e. in a changing environment the social support may result in a potential boost of the production and the performance of some individuals may be reflected in a faster growth. On one hand, our results comply with previous studies indicating the presence of personality types that seemed based on innate traits (Brelin et al. 2005; Castanheira et al. 2013b; Huntingford 1976; Martins et al. 2012; Millot et al. 2014; Øverli et al. 2004). On the other hand, personality types can be modified by the influence of other group members (Magnhagen and Staffan 2005; Magnhagen 2007; Magnhagen and Bunnefeld 2009).

Such disparity of results may be due to species-specific behaviour and/or to previous experiences (e.g. social experiences) that fish were exposed prior to the start of the experiments. Frost et al. (2007) suggested that social context is an important modulator of coping styles in rainbow trout. These authors showed in which, previous positive and negative experiences affect personality and modify boldness. However, shy individuals just alter their behaviour (increase their boldness responsiveness) when their relative competitive ability was similar or higher than their conspecifics. In addition, Ruiz-Gomez et al. (2008) suggest that genetic differences determine social position in early life, whereas some behavioural components of coping styles can be modified by social experience, Moreover, we can also assume that this lack of behaviour consistency measured on proactive and reactive groups, may not represent a "loss" of personality in some individuals, but are instead the reflection of stressors such as social stress. Some species develop strong social hierarchies (Barreto Volpato 2006; Ejike and Schreck 1980; Fox et al. 1997) that may cause changes in personality types according to the available social information in the group. Koolhaas and Boer (2008) showed that groups of proactive individuals may encourage a higher level of aggressiveness and fights so that dominant individuals can keep their position in the group. Taking this in account, we can hypothesise that, after some time it will be difficult to maintain the initial rank position in all individuals, and some of them need to adjust their one personality type in order to balance the social group composition. In reactive groups we can expect that some individual have similar adjustments of behaviour, but in an opposite way. If we think about the adaptive value of aggressiveness such adjustments are logical (e.g. less fight promotes a better welfare of the group). Nevertheless, what are the advantages of these adjustments in alignment with the dimension measure in the present study (the escape response- avoidance)?

It is very likely that some reactive individuals in a group will take this opportunity to express a proactive behaviour in order to have some benefits in the group e.g. a proactive position can promote a major role in the group or greater access to feed, high explorative behaviour and more "creative" mating rituals. According to this, intermediate groups and groups with 1/3 of each personality type could be better balanced, promoting a consistent behaviour shown in this experiment (Figure 1).

Based on our results we could wonder if the individuals that changed the initial personality type (groups of proactive and reactive) by the influence of other group members, might go back to the innate traits when place in intermediate groups or groups with 1/3 of each personality type. Further experiments are needed to determine the plasticity of each personality type under distinct social group compositions.

An alternative/complementary explanation could be that individual differences depend on the social regulation of gene expression, so that different brain genomic and epigenetic states may match with distinct social regulation in behavioural responses, reflecting a higher or lower social plasticity according to the group composition. In fact, Oliveira (2012) proposed an integrative framework for understanding the proximate mechanisms and ultimate consequences of social plasticity. According to this framework, social plasticity is related with biochemically switching of the neural network underlying social behaviour in response to perceived social information. However, the present data set focused on behavioural responses alone. To which extend such mechanisms (brain genomic and epigenetic) are present in fish and contribute to explain behavioural differences in proactive and reactive individuals related with the social group composition still need to be investigated.

This study also showed that the first minute of the restraining test is representative and enough to characterise the three minutes of the restraining test (Figure 2) which may facilitate its use in further personality screening. This finding allows screening in an emerged net during one minute that maybe is less demanding for individuals and researchers with the possibility to screen a large number of individuals in a shorter time period.

The knowledge of personality can help to improve the sustainability and welfare of the aquaculture industry through the establishment of more fine-tuned rearing strategies. Moreover, culture variables could be adjusted in relation to specific group behavioural responses, when designing selection programs.

5. Conclusions

In summary, the results of the present study indicate that homogenous groups of proactive and reactive individuals did not exhibit consistent behavioural responses as opposed to the intermediate and control groups. These results underline the idea that the social contexts in which fish are kept significantly influence personality traits of individuals, which can be modified by the influence of other group members.

Further studies should be addressed to cover both the behavioural and the physiologic mechanisms underlying these differences. A possible extension of this study would be the investigation of the underlying neurological mechanisms that explain distinct social differences related with distinct personality types.

In addition, these results may open up new perspectives for breeding programmes in this species. The traits to be selected deserve further investigation but the social context certainly has influence in the breeding selection and optimization of rearing conditions.

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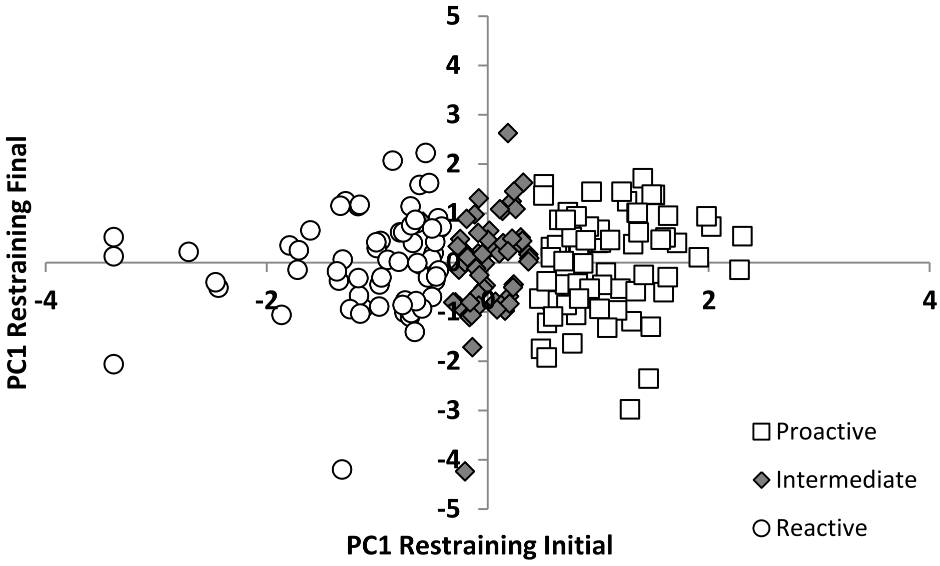
Figure Captions

Figure 1. Relationship between the PC1 behavioural personality scores (initial and final) during net restraining test (A-Proactive; Intermediate; Reactive; B-Control individuals).

Figure 2. Relationship between the PC1 behavioural personality scores during three minutes and the PC1 personality scores during the first minute of the restraining test (A- Initial; B-Final).

Figure 1


PC1 Restraining Final
PC1 Restraining Initial
Proactive
Intermediate
Reactive

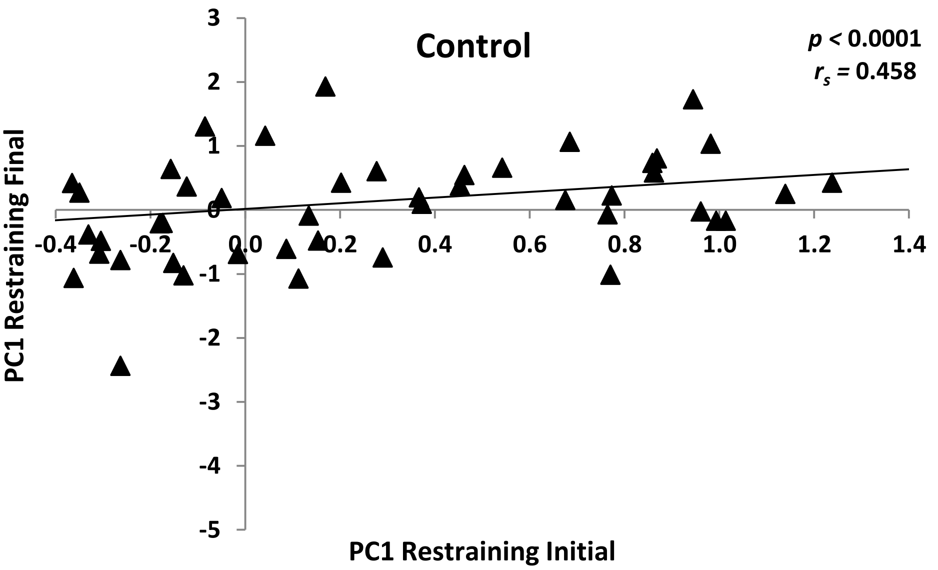
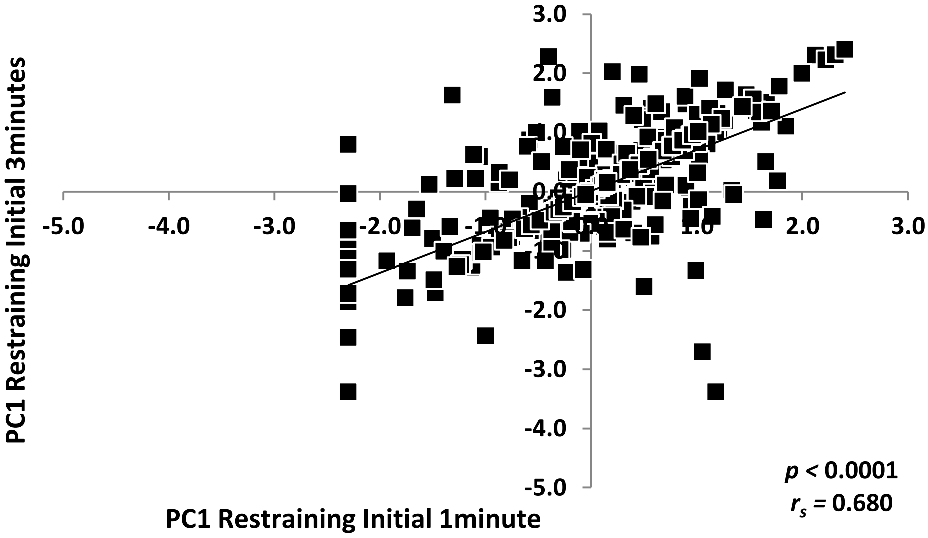
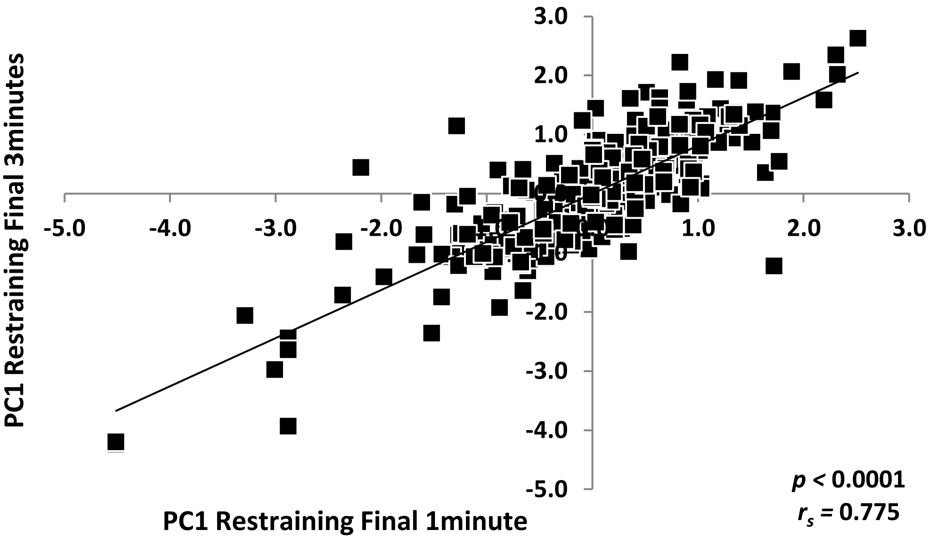

Control
p < 0.0001
r_s = 0.458
PC1 Restraining Final
PC1 Restraining Initial

Figure 2



3.0
2.0
1.0
0.0
-2.0
-3.0
-4.0
-5.0
-5.0
-4.0
-3.0
-2.0
-1.0
1.0
2.0
3.0
PC1 Restraining Initial 3minutes
PC1 Restraining Initial 1minute
$p < 0.0001$
$r_s = 0.680$



3.0
2.0
1.0
-2.0
-3.0
-4.0
-5.0
-5.0
-4.0
-3.0
-2.0
1.0
2.0
3.0
PC1 Restraining Final 3minutes
PC1 Restraining Final 1minute
$p < 0.0001$
$r_s = 0.775$

Tables

Table 1. Mean ± SD, minimum (Min.) and maximum (Max.) values of behavioural variables obtained for the initial restraining test (N = 360) and PCA loading used to generate a principal component scores (PC1).

Behavioural variables	Mean ± SEM	Min.	Max.	Loadings for PC1	% variation explained
Latency escape (s)	18.5 ± 28.0	1	180	-0.709	73.757
Number escape	10.5 ± 7.6	0	35	0.925	
Total escape time (s)	14.2 ± 9.9	0	42	0.924	