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Weak rappers rock more: Hermit crabs assess their own agonistic behaviour.

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Abstract

Fighting animals use a variety of information sources to make strategic decisions. A neglected potential source of information is an individual's own performance during a fight. Surprisingly, this possibility has yet to be incorporated into the large body of theory concerning the evolution of aggressive behaviour. Here we test for the possibility that attacking hermit crabs monitor their own fight performance by experimentally dampening the impact of their shell rapping behaviour. Attackers with dampened raps did not show a reduction in the number of raps used. In contrast, they showed an increased frequency of a less intense agonistic behaviour, shell rocking. This change in behaviour, in attackers that are forced to rap weakly, indicates that they assess their own agonistic behaviour.

Keywords: Contest, assessment, decision, hermit-crab, agonistic, RHP

Introduction

During animal contests information gathering plays a paramount role in critical decisions about whether to initiate and withdraw from a contest [1]. In most cases fighting animals are expected to assess the value of the contested resource [2]. In fights where ‘mutual assessment’ [3] is used they might also assess the fighting ability (resource holding potential, RHP) of their opponent and compare this to their own RHP [4]. Animals using an alternative strategy of ‘self-assessment’ [4] simply continue fighting until a cost-threshold has been reached [5, 6]. In this case, combatants are relying solely on information about their own state. Although fighting animals may switch between these assessment strategies across different phases of a fight [7] and may adjust their behaviour on the basis of previous fights [8], an additional source of information that fighting animals could exploit is their own level of performance within a fight. This may vary from fight to fight and if an individual perceives that it is performing poorly, it could benefit by adjusting its behaviour accordingly. For instance, a poorly performing individual might decide to give up earlier or change tactics.

Hermit crabs, *Pagurus bernhardus*, fight over the ownership of gastropod shells [2], each opponent adopting one of two roles. The smaller crab usually plays the defender role, spending most of the fight tightly withdrawn into its shell. In contrast, attackers grab the defender’s shell and perform bouts of shell rapping, where they strike their own shell rapidly and repeatedly against the shell of the defender in a series of bouts separated by pauses. The fight ends when either the defender allows the attacker to evict it from its shell or if the attacker releases the defender without having evicted it. The defender’s decision to allow an eviction appears to be based on the rate of rapping and the force of impact of the raps it receives. In contrast, when attackers give up, this appears to be influenced by a threshold of accumulated energetic costs [9]. In an experiment where the force of rapping was experimentally damped (by coating the shell surface with an elastic material), evictions were

less likely [10], and successful attackers had to perform more raps to evict defenders. Note that while this treatment reduces the effectiveness of shell rapping, it does not prevent attackers from performing this behaviour. In addition to shell rapping, a second tactic that may be used is shell rocking. Rocking is similar to rapping but appears to be less demanding [11]. Rather than vigorously striking the shells together, the attacker moves the defender's shell back and forth in a slower rocking motion.

Rocking does not appear to be an essential activity that attackers must use in order to secure an eviction, as it is less frequent than rapping and does not occur in all fights. Nevertheless, it is part of the agonistic repertoire of fighting hermit crabs and if attackers can perceive that their raps are ineffective, they might use alternative behaviours such as rocking more frequently. Thus, increased rocking in attackers that rap weakly would provide evidence that they monitor their own performance during fights. Here we test this hypothesis by comparing the frequencies of shell rapping and rocking in fights where the force of rapping had been experimentally dampened against fights without damping.

Methods

P. bernhardus were collected from tide pools at Hannaford Point, UK, and transferred back to the laboratory in Plymouth. They were held in constantly aerated seawater at 15°C on a 12:12h light cycle and fed *ad libitum* on chopped whitefish. Each crab was removed from its original shell (by cracking in a bench vice), sexed and weighed. Only males free from missing appendages or obvious parasites were used in the experiment. To stage fights crabs were allocated to pairs consisting of a larger (potential attacker) and a smaller (potential defender) individual. The larger crab of each pair was provided with a shell that was 50% of its preferred shell weight (determined from previous shell selection experiments relating crab

weight to preferred shell weight [12]), while the smaller crab was provided with a shell that was 100% of the preferred shell weight of the larger crab. In half of the staged fights ($n = 45$) a thin layer (< 0.5 mm) of silicone aquarium sealant was applied over the ventro-lateral surface of the defender's shell, opposite the aperture, corresponding to the area of impact during shell rapping. For the remaining pairs ($n = 45$), the sealant was applied to an area on the dorsal surface of the defender's shell that does not receive rapping. Crabs were then isolated individually overnight (ca. 16h) before fights were held in an arena consisting of a 12cm diameter plastic dish containing aerated seawater as above, placed behind the one-way mirror of an observation chamber. The smaller crab was placed in the arena first followed immediately by the large crab and they were left to interact freely. There was no upper limit for observation time, and fights were allowed to continue until they were resolved, either by the attacker evicting the defender or (in the case of non-evictions) where the attacker released its grasp of the defender's shell following some bouts of shell rapping. Since these fights are non-injurious we did not need to intervene in any staged fight. Shell rapping and rocking and fight outcomes were recorded using The Observer XT 7.0 event recording software. We used logistic regression to determine the effect of dampened shells on the chance of an eviction and on the chance of attackers using shell rocking. We then used two-way ANCOVAs to determine, for those attackers that used rocking, whether the number of raps and rocks (and bouts of these activities) differed between crabs with dampened shells and normal shells, and between outcomes [13]. Although we analyse several response variables we did not use a multivariate test, since this would compress these variables into a single composite response and we are specifically interested in each response variable. Instead we applied a sequential Bonferroni correction to analyses dealing with frequencies of rapping and rocking (Supplement, Table S1). Data were $\text{Log}_{10}(1 + x)$ transformed prior to conducting ANCOVAs. In all analyses the relative weight difference between attackers and defenders (RWD:

[attacker – defender] / mean of attacker and defender) was included as a covariate. In each case there were no significant interactions between RWD and either of the two factors (Supplement, table S2) so these were deleted from the final models reported below. Analyses were performed in the R [14] base package.

Results

Attackers with dampened rapping were less likely to evict the defender ($\chi^2_1 = 7.2, P = 0.01$) (figure 1a) but were not any more likely to use shell rocking than those fighting defenders in normal shells ($\chi^2_1 = 1.7, P = 0.2$) (Figure 1b). For those attackers that used rocking, there was a non-significant trend (after Bonferroni correction) for those with dampened rapping to perform more bouts of rocking ($F_{1,29} = 6.5, P = 0.017$), and they performed more rocks in total ($F_{1,29} = 8.7, P = 0.006$) (Figure 2a) than those where rapping was un-dampened. Further analysis shows that this difference emerged early in the fights, and that attackers with dampened rapping maintained a high level of rocking whereas those with normal rapping reduced the number of rocks as the fight progressed (Supplement, figure S1). Regardless of treatment group attackers that evicted the defender performed more bouts of rocking than those that failed to evict the defender ($F_{1,29} = 9.4, P = 0.005$). There was a non-significant trend for attackers with dampened raps to perform more bouts of rapping ($F_{1,29} = 3.8, P = 0.06$) but there was no effect on the total number of raps ($F_{1,29} = 2.2, P = 0.15$) (Figure 2b). To allow comparison with previous studies of shell rapping we also analysed some additional parameters of the pattern of rapping (Supplement). Here we have focused on the effect of treatment group on agonistic behaviour but the results for all effects are given in table 1.

Discussion

Attackers adjusted their behaviour, by rocking more, when rapping was still possible but its impact was experimentally reduced. In a previous study, attackers with dampened raps performed fewer raps per bout over the course of the fight, a change in behaviour that was attributed to fatigue across longer fights [10]. Here there were also trends for crabs with dampened raps to perform more bouts of rapping with fewer raps per bout. One explanation for increased rocking in attackers with dampened raps could therefore, similarly, experience greater fatigue over longer fights. In this case we would expect tired attackers to substitute shell rapping with less vigorous rocking. However we found no evidence of this because the number of raps and the number of bouts of rapping was not reduced in attackers with dampened raps, and in fact tended to increase. Rather, the extra rocking in the group with dampened raps was performed in addition to shell rapping. Furthermore, if greater rocking was due to fatigue we would expect this pattern to emerge later in the fight but we saw more rocking by attackers with damped raps early in the fights, and this was sustained across the whole fight (Supplement 1). The alternative explanation is that attackers that perceive that they are rapping weakly choose to augment shell rapping with greater and continued use of the additional tactic of shell rocking. Indeed, attackers that evicted the opponent performed more bouts of rocking than those that gave up without effecting an eviction.

There are two ways that attackers might glean information about their own performance. First, they could obtain information directly by assessing the impacts when they strike their shell the defender's shell. Second, they might gather information indirectly by assessing the defender's responses. Although defenders remain withdrawn into their shell for most of the fight, they occasionally extend their chelipeds and walking legs to contact the chelae of the attacker. In fights where this occurs it is usually in defenders that will be imminently evicted, possibly serving as a signal of intent to submit [11]. This behaviour

might therefore provide attackers with information on the effectiveness of their shell rapping. However, it occurs infrequently and usually towards the end of the fight whereas the changes in rocking occurred early in the fight.

Of these two possibilities, the idea that attackers assess the force of impact of their raps seems most aligned with models of fighting based on self-assessment. In contrast, the idea that they adjust their behaviour on the basis of the responses of defenders implies information transfer between opponents, as assumed in models based on mutual assessment. In both types of contest facultative adjustment of agonistic behaviour could be beneficial. A range of extrinsic and intrinsic variables, additional to RHP, are likely to influence an individual's performance during any given fight and these may vary across successive fights. Indeed, both possibilities should be compatible with either mode of RHP assessment, especially for asymmetric contests such as the shell fights described here. In fights settled by self-assessment, information on the opponent's immediate intentions (i.e. to submit) is not necessarily related to the opponent's RHP. In hermit crabs, this information could remain obscured since defending crabs remain withdrawn into their shell for much of the fight. In fights settled by mutual-assessment, where opponents do have information on one another's RHP, an attacker's level of performance during a particular contest could be independent of its RHP relative to that of the opponent. In shell fights, for example, the capacity for an attacker to hit hard is not influenced by any information about the defender.

Current models of fighting [4-6] do not incorporate the possibility that fighting animals might monitor their own performance. The same is true for models of dishonest communication in animal contests, where decisions to exaggerate RHP are based on estimates of RHP distribution across the population, rather than on information about the utility of bluffing within a specific fight [15]. Similarly, recent eco-centric models assume that fighting animals adjust their behaviour on the basis of population-level information about

RHP [16]. In contrast, the idea that fighting animals use feedback on a more immediate scale, concerning their own performance within agonistic encounters, has yet to be incorporated into contest theory. Such information could play a role across the wide range of species and contexts in which fighting has evolved.

Ethics

There are no legal requirements for studies involving decapod crustaceans in the UK, but the work was conducted following the Association for the Study of Animal Behaviour / Animal Behavior Society Guidelines for the Use of Animals in Research.

Data accessibility

Data are available at Dryad doi:10.5061/dryad.j07h2 [17]

Competing interests

We have no competing interests.

Authors' contributions

MB conceived of the study and MB and EE designed the experiment. EE collected the data with assistance from MB. MB and EE analysed the data. MB and EE drafted the manuscript and revisions were undertaken by MB. Both authors gave final approval for publication and agree to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

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Table 1: Effects of treatment group on outcomes and the likelihood and frequency of shell rocking. In part (b) effects that remain significant after corrections for multiple tests have been applied are shown in bold.

(a) Logistic regressions on outcomes and the likelihood of rocking

Effect	Odds ratio	95% CIs (upper, lower)	χ^2	df (N)	P
<i>Likelihood of an eviction</i>					
Group	4.85	1.5, 18.8	7.21	1 (90)	0.01
RWD	6.34	0.7, 77.6	2.52	1 (90)	0.12
<i>Likelihood of rocking</i>					
Group	2.47	0.9, 6.8	1.70	1 (90)	0.20
Outcome	0.64	0.03, 5.7	2.00	1 (90)	0.20
RWD	4.27	0.7, 31.4	2.29	1 (90)	0.13
Group x Outcome	0.48	0.03, 12.7	0.25	1 (90)	0.60

(b) Fight performance (shell rocking and rapping)

Effect	Estimate	SE	F	df	P
<i>Bouts of rocking</i>					
Group	0.258	0.116	6.50	1,29	0.017
Outcome	0.797	0.323	9.40	1,29	0.005
RWD	-0.012	0.252	0.04	1,29	0.83
Group x Outcome	0.423	0.360	1.30	1,29	0.26
<i>Total rocks</i>					
Group	0.327	0.128	8.70	1,29	0.006
Outcome	0.370	0.355	4.04	1,29	0.054
RWD	-0.263	0.377	0.93	1,29	0.34
Group x Outcome	0.019	0.408	0.002	1,29	0.96
<i>Bouts of rapping</i>					
Group	0.125	0.111	3.80	1,29	0.06
Outcome	0.004	0.310	3.60	1,29	0.07
RWD	0.072	0.242	0.21	1,29	0.65
Group x Outcome	0.356	0.354	1.01	1,29	0.32
<i>Total raps</i>					
Group	0.081	0.118	2.20	1,29	0.15
Outcome	0.006	0.372	2.60	1,29	0.11
RWD	0.250	0.255	1.25	1,29	0.27
Group x Outcome	0.311	0.374	0.70	1,29	0.41

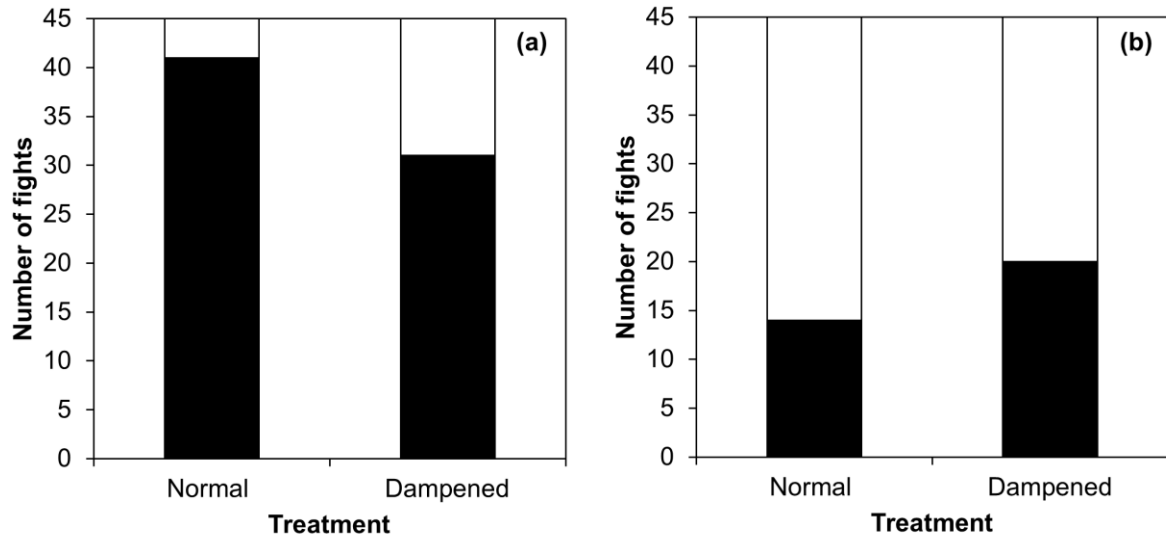


Figure 1: (a) The number of fights that led to evictions (black) and non-evictions (white) and (b) the number of fights where rocking was present (black) and absent (white) for the two treatments.

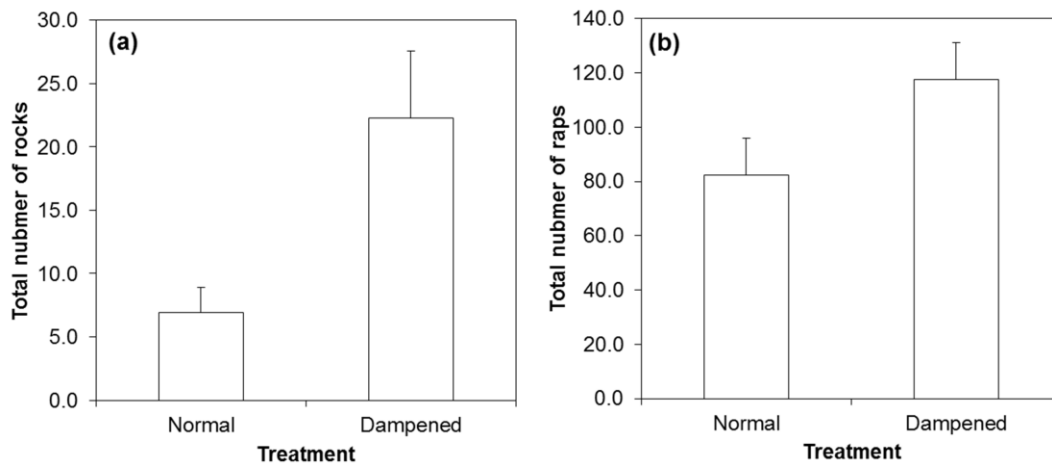


Figure 2. The mean number of (a) rocks and (b) raps performed by attackers using dampened and normal shell rapping. Error bars show standard errors.

Supplementary information

Analysis of the timing of emergence in differences in shell rocking

In order to determine when differences in shell rocking emerged between the two treatment groups (dampened rapping and normal rapping) we calculated the duration of each fight (in seconds) and then divided each fight into quarters. In contrast to the main analysis of the number of rocks totalled over whole fights this yielded a dataset containing observations with zero values, since not all attackers performed rocks in each fight quarter. Therefore, to analyse the effects of group, fight quarter (and their interaction) and RWD on the number of rocks we used a generalized linear mixed model with a Poisson error structure. The fixed factors were the predictors described above and to account for repeated observations from each attacker random intercepts were assigned to attacker ID. This analysis was performed in the lme4 R-package. We used likelihood ratio tests to determine the significance of each effect in the model. Attackers with dampened rapping performed more rocks overall than those with normal rapping ($\chi^2_3 = 9.2$, $P < 0.002$) and there was an overall effect for decreased rocking as the fights progressed ($\chi^2_3 = 53.2$, $P < 0.0001$). A significant interaction between group and fight quarter indicates that this decline was present in attackers that rapped normally but absent in those with dampened rapping ($\chi^2_3 = 70.6$, $P < 0.0001$). To further test the possibility that differences in rocking emerged early in the fight we used a general linear model with Poisson errors to compare the number of rocks performed during the first fight quarter only between the two groups. Although the difference in the number of rocks became more marked as the fight progressed, attackers with dampened rapping performed significantly more rocks than those with normal rapping during this first fight quarter ($\chi^2_1 = 14.3$, $P < 0.0002$). There was no difference in fight duration between the two treatment groups (unpaired t-test: $t_{32} = 1.2$, *NS*).

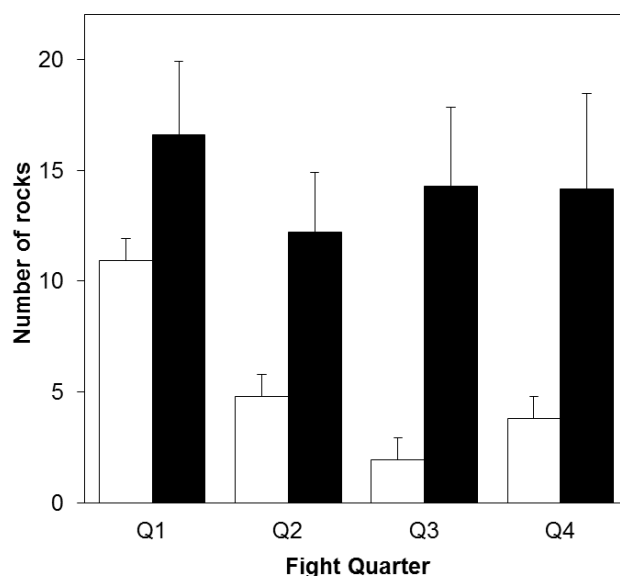


Figure S1. Changes in the number of rocks performed by attackers across fight quarters, for fights where defender's shells were untreated (white bars) and coated with rubber so that attacker's raps were dampened (black bars). Error bars show standard errors.

Analysis of additional shell rapping parameters: Mean number of raps per bout and mean duration of pauses

Analyses were conducted using two-way ANCOVA on Log_{10} transformed data as described in the main text. Attackers in the dampened rapping group performed fewer raps per bout than those with where rapping was not damped ($F_{1,85} = 4.18, P = 0.04$) and the number of raps per bout increased with RWD ($F_{1,85} = 5.50, P = 0.02$). There was no difference in the mean number of raps per bout between outcomes ($F_{1,85} = 0.53, P = 0.47$) and there was no interaction between group and outcome ($F_{1,85} = 0.80, P = 0.40$). Treatment had no effect the mean duration of pauses between bouts of rapping ($F_{1,85} = 1.06, P = 0.30$) but attackers that evicted the defender left shorter pauses than those that failed to evict the defender ($F_{1,85} = 7.73, P = 0.006$). There was no effect of RWD on pause duration ($F_{1,85} = 0.89, P = 0.35$) and there was no interaction between group and outcome ($F_{1,85} = 0.24, P = 0.62$).

Sequential Bonferroni Correction for analyses of shell rapping parameters

Our analyses of shell fighting parameters (including those presented in this supplement) were based on a series of six two-way ANCOVAs, each containing 2 factors plus a covariate. For each factor (i.e. 'Treatment', 'Outcome') we ranked the significance in order of ascending P -values across the set of ANCOVAs. We then calculated adjusted α -values by dividing 0.05 by the number of remaining hypothesis tests in the sequence, starting from the test with the lowest P -value. Thus, the adjusted α -value for the most significant test in the sequence would be $(0.05/6) P = 0.008$, and in order of declining significance they were 0.01, 0.0125, 0.016, 0.025 and 0.05. In table S1 we give the P -values for each main effect, ranked as described, along with the appropriate adjusted α -value and declaration of significance in light of these adjusted thresholds. Note that a more conservative experiment-wide adjustment to $\alpha = 0.008$ would only have changed the significance declaration for one effect, that of outcome upon the number of bouts of rocking. While there is some debate around the necessity for Bonferroni corrections (e.g. Nakagawa 2004), it appears that the less conservative sequential form is the preferred one, as it strikes a better balance between the need to control for Type 1 errors on the one hand while reserving enough statistical power to avoid Type 2 errors on the other (Nakagawa 2004). As recommended (Nakagawa 2004), we have included our non-significant results in this study and from the table below it can be seen that (in this case) their inclusion does not inflate the chance of Type 2 errors.

Table S1. Response variables ranked by ascending *P*-value grouped by predictor (Group or Outcome), with sequentially adjusted α -values. For effects that were significant prior to Bonferroni correction for multiple testing, a declaration of significance following correction is given. Effects that were not significant prior to correction are shown in grey text.

Response variable	<i>P</i>-value	Adjusted α-value	Significant
<i>Predictor = Treatment (dampened/un-dampened)</i>			
Total rocks	0.006	0.008	Yes
Bouts of rocking	0.017	0.01	No
Raps/bout	0.04	0.0125	No
Bouts of rapping	0.06	0.016	
Total raps	0.15	0.025	
Duration of pauses	0.19	0.05	
<i>Predictor = Outcome (eviction/non-eviction)</i>			
Duration of pauses	0.006	0.008	Yes
Bouts of rocking	0.005	0.01	Yes
Total rocks	0.051	0.0125	
Bouts of rapping	0.07	0.016	
Total raps	0.11	0.025	
Raps/bout	0.45	0.05	

Analysis of interaction effects involving the covariate (RWD)

Since the interpretation of main effects in ANCOVA depends on heterogeneity of slopes across the covariate, prior to conducting the main analyses reported in the Results section of the main text we first tested for interactions between RWD and Treatment Group and RWD and Outcome. None of these interactions were significant (table S2) so they were deleted from the models and the models recalculated.

Table S2: Testing for interaction effects between factors and the covariate (RWD) in ANCOVAs (corresponds to analyses in table 1b in main text).

Effect	F	df	P
<i>Bouts of rocking</i>			
Group	6.1	1,27	0.02
Outcome	8.8	1,27	0.006
RWD	0.04	1,27	0.84
Group x Outcome	1.2	1,27	0.28
Group x RWD	0.12	1,27	0.72
Outcome x RWD	0.14	1,27	0.71
<i>Total rocks</i>			
Group	8.1	1,27	0.008
Outcome	3.8	1,27	0.61
RWD	0.88	1,27	0.36
Group x Outcome	0.002	1,27	0.96
Group x RWD	0.05	1,27	0.82
Outcome x RWD	0.29	1,27	0.59
<i>Bouts of rapping</i>			
Group	3.8	1,27	0.06
Outcome	3.6	1,27	0.06
RWD	0.21	1,27	0.65
Group x Outcome	1.03	1,27	0.32
Group x RWD	0.0003	1,27	0.99
Outcome x RWD	2.55	1,27	0.12
<i>Total raps</i>			
Group	2.33	1,27	0.14
Outcome	2.79	1,27	0.11
RWD	1.32	1,27	0.26
Group x Outcome	0.73	1,27	0.40
Group x RWD	0.47	1,27	0.50
Outcome x RWD	3.33	1,27	0.08

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