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Social competition stimulates cognitive performance in a sex-specific manner

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Social interactions are thought to be a critical driver in the evolution of cognitive ability. Cooperative interactions, such as pair bonding, rather than competitive interactions have been largely implicated in the evolution of increased cognition. This is despite competition traditionally being a very strong driver of trait evolution. Males of many species track changes in their social environment and alter their reproductive strategies in response to anticipated levels of competition. We predict this to be cognitively challenging. Using a *Drosophila melanogaster* model, we are able to distinguish between the effects of a competitive environment versus generic social contact by exposing flies to same-sex same-species competition versus different species partners, shown to present non-competitive contacts. Males increase olfactory learning/memory and visual memory after exposure to conspecific males only, a pattern echoed by increased expression of synaptic genes and an increased need for sleep. For females, largely not affected by mating competition, the opposite pattern was seen. The results indicate that specific social contacts dependent on sex, not simply generic social stimulation, may be an important evolutionary driver for cognitive ability in fruit flies.

1. Introduction

Cognition is defined as the neural processes needed to acquire, process, retain and use information [1], including processes such as learning, memory and decision making [2]. However, while the processes by which brains have evolved and how the environment affects the cognition of animals have been widely researched, a consensus about the critical drivers of cognitive evolution has not yet emerged [3].

Social contact has long been hypothesized to affect the evolution of cognition [4]. The social brain hypothesis postulates that the evolution of improved cognition is driven by increasing social group complexity [5]. However, types of social interactions are varied and which are important for cognition to evolve is controversial [5,6]. The role of sexual competition, in particular, has proven to be problematic. In mammals, an increase in the sexual competition was shown to have no, or a negative effect on brain size, the notional proxy for cognitive ability [7]. However, in frogs [8] and pipefish [9], differing levels of sexual competition has been associated with morphological differences in brain structure. Similarly, in the rose bitterling, plastic male mating strategies are associated with the cognitive performance [10], and in bowerbirds increased complexity of displays correlates with an enlarged cerebellum [11]. In addition, in species where females are under sexual selection instead of males they display heavier brains [9]. In the fruit fly (*Drosophila melanogaster*) and seed beetle (*Callosobruchus maculatus*), enforced monogamy over multiple generations reduces cognitive performance compared to males kept in polygamous conditions [12,13]. As the social environment is dynamic, males need to assess and predict competition after mating (sperm competition), which is likely cognitively challenging. Indeed, it is predicted to be an evolutionary

driver of the ability to assess quantity i.e. the magnitude of competition within the environment (quantity estimation [14]).

In *D. melanogaster*, males alter their mating duration and ejaculate [15,16] in response to exposure to other males, a cue of future sperm competition threat. Males can track changes in their social environment and are sensitive to the amount of time spent with other males [17]. Males also alter ejaculate depending on the number of males in the environment [18]. This sophisticated, multifaceted response requires males to assess the magnitude of competition akin to quantity estimation [14]. The response requires multiple sensory inputs [19] and uses processes known to be important in learning and memory [17]. We therefore hypothesized that competitive sexual interactions may be a vitally important social driver of cognitive ability in male *D. melanogaster*.

Any form of environmental enrichment could be cognitively stimulating [20], so to determine whether social reproductive competition cues are particularly important, we compared responses to conspecifics and heterospecifics. *Drosophila* live in multiple species groups [21], and this requires the ability to interpret different forms of social contact. *D. virilis* and *D. melanogaster* are generalists and are expected to compete for food and/or space [22]; however, they are very distantly related and are likely to be fully reproductively isolated as this is seen between more closely related species [23]. Indeed, *D. melanogaster* males do not make a sperm competition response to *D. virilis* males [24], indicating they do not perceive them as a reproductive threat. Therefore, any differences seen in *D. melanogaster* males after contact with conspecific males not seen due to contact with heterospecific contact are suggestive of the importance of sexual competition.

Female and male social mechanisms are thought to differ [25]; therefore, we also studied the effects of conspecific and heterospecific same-sex social contact in females. As females do not undergo the same sperm competition pressures, it was expected that any difference shown by females in response to conspecific contact would be mirrored when exposed to heterospecific social contact.

We used multiple assays of olfactory and visual learning and decision-making ability of males and female flies held in isolation or exposed to a conspecific or heterospecific social partner. To assess potential underlying molecular mechanisms, we measured changes in the expression of genes associated with synaptic plasticity at the neuromuscular junction (*Neurexin-1* [26]), growth (*Futsch* [27]) or maintenance (*Bruchpilot* [28]) and that we had previously identified to be socially responsive in male-male contact [29]. We also assessed how activity patterns changed depending on the social environment, as this is associated with sleep and cognitive processes.

2. Materials and methods

(a) Fly stocks and rearing

Drosophila melanogaster fruit flies were raised in a 25°C humidified room, with a 12 : 12 light : dark cycle. Flies were maintained in plastic vials containing 7 ml sugar-yeast-agar medium [30]. Wild-type flies are from a large laboratory stock population of the Dahomey strain [31]. Larvae were raised 100 per vial and supplemented with live yeast. As *Drosophila virilis* have a slightly lower thermal preference than *D. melanogaster* [32], *D. virilis* were grown in vials at 20°C before collection. Upon eclosion, sexes were separated using ice anaesthesia. Non-focal flies were collected in single-sex

groups of ten and the females supplemented with live yeast. All focal flies were aged individually for 1 day before exposure to a social partner. Non-focal flies used as social partners were aged-matched and identified with a small wing clip.

Flies were maintained in their social treatments, singly, with a conspecific or a heterospecific of the same sex, for 10 days before being used in one of the assays detailed below (electronic supplementary material, figure S1). We assessed learning in a range of assays, both sexual and non-sexual context. Where possible, the observer was blind to the social identity of the focal fly.

(i) Virgin finding—decision making in a complex environment

We tested a male's decision making in a complex social environment, whereby males target courtship towards a virgin female in a group of mated females [12]. Focal males were aspirated into a group of six females, one virgin and five mated 24 h prior. Male courting behaviour was recorded every minute for 20 min or until mating occurred. The female type was identified by a wing clip administered 2 days before a trial. Virgin females were clipped in 50% of the trials. Trials were conducted on 10 individuals at a time, five of each social treatment, to control for time of day effects. This assay was carried out at 25°C under standard white light. Each block contained 30 males from each social treatment and was repeated three times, with separate experiments for conspecific and heterospecific contact.

(ii) Aversive olfactory associative learning

We tested the ability of flies to learn to associate an odour with a mechanical shock [33]. Experiments were performed at 22–25°C under red light to remove visual cues. Odorants, 3-octanol (2.7 µl ml⁻¹) and 4-methylcyclohexanol (1 µl ml⁻¹) diluted in light mineral oil, were drawn through a T-maze with a vacuum pump. The side the odorant originated from was switched every second trial.

Firstly, an innate preference for either odour was derived from the time spent in either arm (not the central section of the T maze) over 2 min. A fly was then conditioned to avoid its preferred odour by exposing it to the preferred odour accompanied by mechanical shock for 1 s every 5 s for 1 min. This was followed by a 30 s exposure to air and then 1 min exposed to the non-preferred odour without shock. This training protocol was repeated once. To test learning, flies were immediately moved to the central section choice point and given both odours simultaneously. The time an individual spent showing a preference for either odour was recorded over 2 min. A learning index (LI) was calculated as (post-training time in unconditioned odour ÷ post-training total time making a choice) – (pre-training time in unconditioned odour ÷ pre-training total time making a choice).

Each testing period assessed 2–8 flies, half held singly, repeated 6–8 times per social treatment. To control for day and time effects, the LI of individuals kept with social partners was standardized by the average LI of singles in the same block. Separate experiments were conducted for conspecific and heterospecific exposure.

(iii) Visual learning and reversal learning

This assay tests the ability of flies to associate a visual cue, a green dot, with a 'safe' temperature zone on the floor of an arena. Learning was assessed as the time a fly took to spend 20 s consecutively in the 'safe' zone. The total distance travelled by the fly was measured to control for directional learning. An increase in distance travelled would suggest that flies were not learning visual cues, but were instead learning the presence of a safe spot within the arena. Flies underwent three trials of 10 min. A reversal 'probe' trial was then performed by moving the visual cue to an 'unsafe' area of the arena and measuring

the time taken to spend time in the 'safe' zone and the mean distance from the visual cue.

(iv) Gene expression

Flies were snap frozen in liquid nitrogen, head and thorax dissected away from the abdomen on dry ice and frozen at -80°C before extraction. RNA was extracted from a pool of 10 to 25 flies using Direct-zol RNA miniprep columns. cDNA was synthesized using the Life Technologies First-strand cDNA kit. Housekeeper genes *EF1* and *Rap21* were chosen as likely to be unaffected by the social environment [34].

Quantification of transcript levels relative to housekeeping genes was performed using the Pfaffl method [35]. Ct values for samples were quantified against the lowest value across 5 to 7 biological replicates, taking into account the efficiency of the primer used. Relative expression was calculated by dividing the gene of interest by the geometric mean of the housekeepers for each sample, averaged across biological replicates [35].

(v) Behavioural analysis—activity, social interactions and aggression

We observed the behaviour of flies within their social treatments. Focal flies were held in their social treatment for 5 days and behaviour recorded on days 6, 8 and 10, at 9.00, 12.00 and 15.00. This was replicated in four blocks; each block contained 10 vials per sex and social treatment (final $n = 40$). Focal flies were scored as active or not, and for those with a social partner, whether they were within one body length of that partner (proximity) and whether the flies interacted aggressively (wing flicking and fencing) (females [36], male [37]) once every 5 min for 10 s. Movement and proximity were not mutually exclusive; individuals could be both stationary and close to another flies. However, any aggressive interactions were deemed as activity whether flies were stationary or not. For this assay, it was impossible to blind the observer to the social treatment of the fly.

(b) Data analysis

Statistical analysis was performed using SPSSv14 and R 3.3.1 [38].

(i) Virgin finding—decision making in a complex environment

To account for day/time of day effects, amount of time courting and courtship directed to the virgin for paired flies was standardized by subtracting from each, the mean of their matched single counterparts. This was then analysed using a generalized linear mixed model (GLMM) with a binomial distribution. Social treatment was a fixed factor and ID of the fly nested in repeat as a random factor. A model with the effect of social treatment included was compared to that only containing random factors using analysis of deviance.

(ii) Aversive olfactory associative learning

To account for day/time of day effects, innate odour preference and LI (equation (2.1)) for flies kept with a social partner were standardized by matched groups of single flies tested concurrently. Standardized values were then compared to 0 (i.e. no difference between single and social partners) with one sample Wilcoxon signed-ranks tests.

(iii) Visual learning and probe trial analysis

A learning index was calculated for both time taken to find a 'safe' spot and for the total distance moved by subtracting the last learning trial from the first learning trial. The time taken to find a 'safe' spot was compared between individuals kept with a conspecific or heterospecific social partner with Mann–Whitney U tests. For total

distance moved, the difference between the first and last trial was compared to zero with a Wilcoxon signed-rank test.

To test for learning in reversal trials (both time taken to find 'safe' spot and mean distance from 'safe' spot), learning was calculated as the difference between an individual kept with a social partner and the average of individuals kept singly. Both measures were compared to 0 (no difference between single and social partner males) with a one sample *t*-test.

(iv) Gene expression

Relative expression differences were examined using ANOVA with gene identity and social group as fixed factors. Pairwise comparisons with Bonferroni correction were performed to investigate the difference between males kept singly and with a social partner for each gene.

(v) Social interactions and activity

Separate analysis was conducted for each sex. Movement, proximity and interaction data were analysed with GLMM with zero inflation correction (package glmmADMB and glmmTMB). For movement, social treatment and time of day were used as fixed effects, and day and ID were random effects. The number of interactions with social treatment and time as fixed factors, day and ID as random effects. Maximal models were reduced to minimum explanatory factors through analysis of deviance, with post-hoc comparisons between groups performed using the package means with the Tukey adjustment for multiple testing.

3. Results

After exposure to a conspecific, males performed better in both the virgin finding assay (AOD: $\chi^2_1 = 29.212$, $n = 165$, $p < 0.001$; figure 1*a*) and olfactory learning ($z = 2.753$, $n = 58$, $p = 0.006$; figure 1*b*) compared to males held singly. There was a similar (though non-significant) trend for visual reversal learning (time: $z = 1.851$, $n = 19$, $p = 0.064$; distance: $t_{18} = 0.994$, $p = 0.355$; electronic supplementary material, figure S3A and B). Males kept with heterospecifics responded to social contact through an increase in courting effort (AOD: $\chi^2_1 = 4.871$, $n = 176$, $p = 0.027$; electronic supplementary material, figure S2) but showed none of the learning improvements seen when males were kept with conspecifics when compared to single males (virgin finding: $\chi^2_1 = 8.1616$, $n = 176$, $p = 0.004$; figure 1*a*; olfactory learning: $z = 0.957$, $n = 30$, $p = 0.338$; figure 1*b*; visual reversal learning time: $z = -1.461$, $n = 18$, $p = 0.144$; distance: $t_{17} = 0.115$, $p = 0.115$; electronic supplementary material, figure S3A,B). Importantly, the ability of males to detect cues needed to complete the learning tasks did not differ significantly between social environments (electronic supplementary material, figure S4).

Females did not statistically differ in olfactory learning ability when kept with conspecifics ($t_{30} = -0.308$, $p = 0.760$; figure 1*c*) but significantly improved when exposed to heterospecifics ($t_{32} = 2.675$, $p = 0.012$; figure 1*c*). However, this may be partly due to a change in female olfaction preference for training odours used in the assay. Females significantly changed their preference for 3-octanol compared to single females when kept with both conspecifics ($z = -2.079$, $n = 31$, $p = 0.038$; electronic supplementary material, figure S5A) and heterospecifics ($z = 2.010$, $n = 33$, $p = 0.044$; electronic supplementary material, figure S5A). There was no statistical difference in visual reversal learning dependent on social treatment (conspecific time: $z = -1.492$, $n = 19$, $p = 0.136$; distance:

Figure 1. Effect of social environment on learning. (a) Change in percentage courting directed towards a virgin female ('correct' courting) by males kept with *D. melanogaster* or *D. virilis* rivals. Change in olfactory learning ability of (b) males or (c) females kept with *D. melanogaster* or *D. virilis* partners. All data are standardized by comparison to the group average of single flies assayed at the same time. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

$\chi^2_1 = 0.604$, $n = 19$, $p = 0.546$; heterospecific time: $z = 1.099$, $n = 14$, $p = 0.272$; distance: $\chi^2_1 = 2.291$, $n = 14$, $p = 0.022$; electronic supplementary material, figure S3C,D).

We found a general pattern of increased expression across all genes in males kept with conspecifics compared to single males ($F_{1,29} = 11.349$, $p = 0.002$; figure 2a). *Post hoc* analysis showed both *futsch* ($t_9 = -3.299$, $p = 0.012$) and *Neurexin-1* ($t_{10} = -3.424$, $p = 0.006$) were significantly upregulated in males kept with conspecifics. Expression did not significantly differ between males held singly or with heterospecific males ($F_{1,22} = 2.589$, $p = 0.122$; figure 2b). Female gene expression was not affected by conspecific contact ($F_{1,24} = 3.351$, $p = 0.080$; figure 2c). However, females kept with heterospecifics significantly increased expression overall ($F_{1,24} = 8.209$, $p = 0.009$; figure 2d), though not for individual genes after *post hoc* testing.

The male movement was dependent on an interaction between social environment and time of day ($\chi^2_4 = 11.297$, $p = 0.004$; electronic supplementary material, figure S6A). Males with conspecifics moved less than males kept singly and with heterospecifics. Conspecific partners were significantly closer in proximity than heterospecific partners ($\chi^2_1 = 11.575$, $p < 0.001$; electronic supplementary material, figure S6B) and also interacted significantly more ($\chi^2_1 = 31.94$, $p < 0.001$; electronic supplementary material, figure S6C).

Females held with any social partner moved less than single females ($\chi^2_4 = 10.761$, $p < 0.004$; electronic supplementary material, figure S7A). Females kept with conspecifics moved less than single females at 9.00 only ($t_{334} = 2.666$, $p = 0.0219$), while with heterospecifics they were less active at 9.00 ($t_{334} = 2.504$, $p = 0.034$) and 12.00 ($t_{334} = 3.248$, $p = 0.003$). Type of social contact did not affect partner proximity ($\chi^2_1 = 0.4253$, $p = 0.514$; electronic supplementary material, figure S7B). Interactions were seen too infrequently to analyse.

4. Discussion

Our data support the idea that competitive interactions, specifically mating competition, is important for male cognitive ability. Males exposed to conspecifics, but not heterospecifics that acted as general social contact, showed a general cognitive improvement, including in a visual learning task, a sensory modality not required for a response to sperm competition [19]. Interestingly, the opposite pattern was true for females who increased olfactory learning ability in response to exposure to heterospecifics but not conspecifics.

When exposed to a conspecific, males increased their ability to identify a virgin female. Though males exposed to heterospecifics failed to improve within this assay, they did increase courtship effort. *D. melanogaster* males increase the volume of their courtship song after social contact [39] and experience of heterospecifics strengthens conspecific mating preferences [40]. In line with this, our results reflect that social experience increases male's preference for conspecifics. Indeed, males involved in virgin finding, although requiring learning, would also be expected to draw on other cognitive processes that could lead to a change in social preference.

Social environments that produced increases in learning ability for both sexes were associated with increased expression of synapse-related genes and a decline in movement (used as a proxy for sleep). Decreases in synapse number are linked to decreased cognition in multiple species [41], and chemically induced increases in synapse connectivity in mice improve cognitive performance [42]. Sleep is thought to be vital in developing and consolidating synaptic circuitry [43,44]. Consistent with this, *Neurexin-1*, a gene involved in synaptic plasticity, is significantly increased in heads when males are kept with conspecifics. *Neurexin-1* acute overexpression in adulthood is associated with synaptic growth and an increase in sleep in

Figure 2. Gene expression changes depending on social environment. Males (a and b) or females (c and d) were held singly (white bars) or with social partners (grey bars) that were conspecific (a and c) or heterospecific (b and d). Significant effects are indicated across the whole model or in pairwise comparisons where * p < 0.05, ** p < 0.01, *** p < 0.001.

D. melanogaster [45]. In this study, we cannot separate out the exact mechanisms leading to an increase in learning. However, we observe a coordinated change in activity patterns and increased the expression of genes involved in synaptic growth [45] due to changes in the sexual environment, suggesting the socio-sexual environment has a significant role to play in cognitive development.

Females also display less movement (probably more sleep) and an increase in synaptic gene expression when kept with the type of contact leading to an increase in learning, in this case heterospecific. We interpret the male responses caused by conspecific contact response to the sperm competition environment [15], however, what may be causing females to increase memory after contact with heterospecifics is unknown. In addition to an increase in learning, females were found to have changed their olfactory preference in response to heterospecific exposure. During the assay, this preference was taken into account by training individuals against their preferred odour. However, the change would also suggest heterospecific partners could impact future choice influenced by smell, for example, of oviposition sites [46]. Female *D. melanogaster* use learning and memory processes to choose oviposition sites avoiding parasitism [47] and for preferred substrates [48]. Cues of heterospecific competition may similarly affect female *D. melanogaster* egg-laying decisions, though this is yet to be tested.

Examples of difference in cognitive abilities between the sexes are relatively common [49,50] and are often connected to sexually specific fitness benefits arising from different

selective pressures [10]. Here, cognitive differences are seen in how the sexes react to different same-sex social pressures. This serves to again highlight that sexual competition is especially important for males to develop cognitive abilities. It also suggests that cognitive evolution is driven by sex-specific pressures in *D. melanogaster*. Indeed, female *D. melanogaster* base some mating decisions on public information [51], whereas males only seem to use cues directly related to their own experience to modulate behaviour [52]. In insects, the evolution of cognition is intimately linked to the increasing complexity of mushroom bodies, a structure which is analogous to the mammalian central cortex [53], leading to greater behavioural complexity [54,55]. Previously, the primary driver of cognitive development in insects was thought to be complex foraging behaviour [56]. Here, we present evidence that intra-sexual competition, and specifically sperm competition responses previously linked to the mushroom bodies [17], are also likely to be important in driving cognitive development in males. We also find that cues of another species may drive female cognitive development, though we know much less about the underlying processes. Overall, our data, together with other recent studies [10,12], highlight competitive interactions as a key social driver of cognitive evolution [4,5], at least outside of mammals. We therefore suggest the requirement for plasticity in male and female responses to fluctuating socio-sexual environments may be more generally important to cognitive development than previously thought.

Data accessibility. The datasets generated and analysed during the current study are available in the open access Dryad Digital Repository <https://doi.org/10.506/dryad.gqnk98sk4> [57].

Authors' contributions. J.R. designed experiment, carried out laboratory work, analysed data and drafted the manuscript; L.M. carried out laboratory work, contributed to analysis and drafted manuscript; Z.M. contributed to analysis; E.J.D. contributed to analysis, drafted the manuscript and provided supervision to J.R.; A.B. designed experiment, drafted the manuscript and provided supervision to

L.M. and J.R. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

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