Section: Cognitive Neuroscience & clinical and Translational Neuroscience

Title: **Do wholes become more than the sum of their parts in the rodent (*Rattus Norvegicus*) visual system? A test case with the Configural Superiority Effect**

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Abstract:

The rodent has been used to model various aspects of the human visual system, but it is unclear to what extent human visual perception can be modelled in the rodent. Research suggests rodents can perform invariant object recognition tasks in a manner comparable to humans. There is further evidence that rodents also make use of certain grouping cues, but when performing a shape discrimination they have a tendency to rely much more on local image cues than human participants. In the current work, we exploit the fact that humans sometimes discriminate better between whole shapes, rather than the parts from which they are constructed, to ask whether rodents show a classic Configural Superiority Effect. Using touch-screen equipped operant boxes, rats were trained to discriminate "part" or "whole" images based off of those used by Pomerantz et al. (1977). Here we show that rats show no advantage for wholes and that they perform better when presented with simpler image parts, a pattern of effect opposite to what was seen in humans when highly comparable stimuli were used. These results add to our understanding of the similarities and differences between the human and rodent visual system, and suggest that the rodent visual system may not compute part whole relationships in a way comparable to humans. These results are significant from both a comparative anatomy perspective, and of particular relevance for those wishing to use rodents to model visuo-perceptual deficits associated with human psychiatric disorders.

Introduction:

For over 100 years psychologists have documented principles defining how visual input is organized. For example Gestalt psychologists documented that visual input is grouped in accordance with a number of heuristics, such that parts of the image that are close together, similar in colour, or moving in the same direction are more likely to be grouped together (Wagemans *et al.*, 2012). Gestalt psychologists also documented several perceptual phenomena in which the grouping of a number of parts led to the percept of a whole that could not be predicted as a simple linear summation of those parts (Wertheimer *et al.*, 1961). These observations inspired the formulation that 'the whole is different to the sum of its parts'. This was elegantly operationalized in a 'Configural Superiority' paradigm (Pomerantz *et al.*, 1977) that showed the orientation of a line was more accurately and more rapidly detected among other distractor lines when the target and distractor lines were combined with a context of two additional (technically uninformative; Figure 1) lines. This phenomenon is striking because neurones in early visuals areas in the primate visual system will produce action potentials in a selective manner to edges of a particular orientation and frequency (Skottun *et al.*, 1991; Lamme, 1995; Hubel & Wiesel, 2009). In contrast neural responses that are selective to more complex configural properties, such as shape, are only found in higher areas of the primate visual system (Pasupathy & Connor, 2002). Thus, while edges appear to be represented early in the processing of visual input in primates, they are less perceptually accessible than the 'shapes' extracted later in the processing hierarchy in this paradigm. This, and similar demonstrations, have led to the 'reverse hierarchy theory' of human visual perception(Hochstein & Ahissar, 2002) which argues that our experience of the visual world is based upon a rapid feed forward extraction of complex features (such as objects and scenes), and that access to the "parts" from which those complex wholes are constructed requires a more effortful and attention driven process.

The availability of non-human models of the Gestalt phenomena is limited, and the neurobiology of these processes is poorly understood. Furthermore, it is now recognized that visual perception is disrupted in numerous disorders of the central nervous (Butler *et al.*, 2008; Kirby *et al.*, 2010; Robertson *et al.*, 2014) system. Accordingly, the goal of this work was to determine if rats would display a configural superiority effect when tested in touch-screen equipped operant boxes using stimuli very similar to those used in seminal human studies of the phenomena. To do this rats were trained to discriminate either a "part" (a simple line orientation) or a "whole" (a line orientation combined with additional non-informative information) to earn a food pellet reward. The rate of learning was the primary measure of accuracy in these studies (Bussey *et al.*, 2008; Fellini *et al.*, 2014). Moreover animals were tested with "big" or "small" stimuli to confirm that the observed effects were not a function of the size of the image used.

Materials and Methods

Animals

All animals were treated in accordance with the European Ethics Committee (decree 86/609/CEE), the Animal Welfare Act (1 USC 2131) and the Guidelines for the Care and Use of Mammals in Neuroscience and Behavioral Research (National Research Council 2003). The study protocol was approved by the local animal experimental ethical committee at Janssen Research and Development (Beerse, Belgium).

Male Lister-Hooded rats (*Rattus Novergicus*; Harlan, Netherlands: 180-200g at arrival) were used for all work reported with this manuscript. 24 animals were used in each study (N=48), with 12 animals being assigned to the "Whole" or "Part" conditions in each study The assignment to each condition was based on the number of sessions it took an animal to reach the final "pre-training" criteria of making 60 responses at the illuminated window (altering locations between sessions) within 30mins. In this way each group had a similar number of "fast" and "slow" learners at the start of the experimental phase of the study. Upon arrival animals were housed four per cage in individually ventilated type four cages (1400cm2). These cages were filled with sawdust and animals were also given chew blocks and red plastic tunnels. Rats were fed daily after testing and given enough food to maintain them at 85-90% of free feed body weight (typically 15grams a day). Animals were given free access to water except during testing. Upon arrival animals were given one week to acclimatize to their new setting before being placed on food restriction. Animals were typically trained once daily, 5 days a week, and fed after testing.

Apparatus

All experiments were performed in modified Med Associates operant chambers (Med associates Inc. Fairfax, Vermont; H 33.5 x W 32.5 X L 40 cm). Each chamber was equipped with a pellet receptacle containing an infra-red nose poke detector and reward light, as well as a pellet dispenser, tone generator and house light. The opposite wall of the chamber was replaced with a touch-sensitive computer monitor that was partly covered with a mask restricting responses to two areas on the screen. A counter weighted "flap" (5x36 cm) was placed in front of the screen to slow the response of the rat. The floor consisted of aluminium bars spaced approximately 1 cm apart. Each chamber was housed in a sound attenuated chamber (60 x 74 x 60 cm) fitted with a small ventilation fan. Screens and boxes were controlled by K-limbic software (K Limbic, Sawbridgeworth, UK).

Stimuli

The stimuli (white portion) used in experiment 1 were approximately 4cm^2 although the response area was considerably larger. The part stimuli consisted of single lines at approximately ±45° rotation from vertical. In contrast the whole stimuli were comprised of the same lines used in the part stimuli but with an "L" shape component added. One image was used per study.   The stimuli used in experiment 2 were approximately 8cm^2 and covered the response area in its entirety (Figure 1).
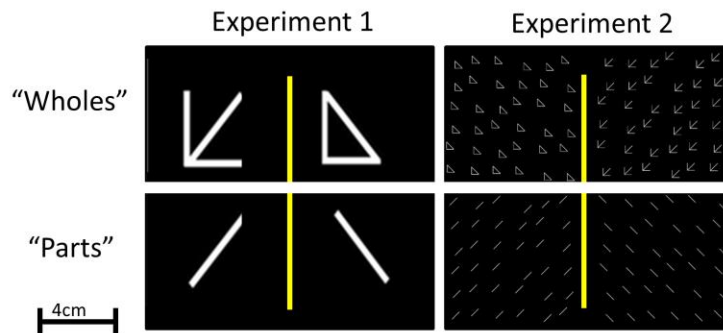
Figure 1, Stimuli used in experiments 1 and 2.

The stimuli in experiment 2 were made of the same shapes used in experiment 1 except they were now smaller and displayed repeatedly upon the screen. In experiment 2, 10 different stimuli with slightly different (jittered) spatial positions were used in each condition to ensure that rats learned to respond based on the individual components of the stimuli rather than the space or pattern of the components of the stimuli (Figure 1).

Training

Studies 1 and 2

Pre-training

Animals were prepared for training on the visual discrimination task in a stepwise manner. Animals were initially encouraged to explore the test chamber by placing a mixture of peanut butter and reward pellets upon the screen. This was typically done for two days, or as long as it took for all animals to eat the mixture from the screen within a 30min session (most animals would eat from the screen after two days). Animals were then trained to associate the sounding of a tone with a delivery of food pellet reward. This was done by pairing the delivery of a food pellet with a tone (0.5s) and activation of the pellet receptacle light. Once the pellet was collected, a 30s inter-trial interval (ITI) was started. At the end of this interval another pellet would be delivered. A session lasted for 60 trials or 60 minutes, whichever occurred first. Rats usually only required 1 session to make the association

between the tone and the delivery of a pellet reward. Once this behaviour had been acquired rodents were trained to press an illuminated area upon the screen to earn a food pellet reward. Initially the whole screen was illuminated, so a response at any place upon the screen would be rewarded. Once a response was made at any part of the screen, the screen would go dark, a tone would sound, the magazine light would turn on, and a food pellet would be delivered. Collection of the pellet would cause the magazine light to turn off, and start a short ITI (10s). Once the ITI had passed, the magazine light would again be illuminated. A response at the magazine would cause the light to turn off, and the screen to again be illuminated, starting the next trial. A session lasted for 60 trials or 60 mins, whichever occurred first (this typically took 1 or 2 days). Once animals were reliably pressing the screen to earn a food pellet reward, the illuminated area of the screen was reduced to just half of the screen (divided along the vertical), and only a response at this illuminated portion of the screen would result in a food reward (responses at the non-illuminated portions of the screen had no consequence). Once animals had learned this (typically 1 day), they were then placed on an identical version of the task, except now the illuminated target area switched between two distinct locations on the screen from trial to trial in a random fashion (one day). Responses at the un-illuminated locations had no consequence. Animals were then considered ready to be put on the full discrimination task. Animals were divided between the experimental groups based upon how long it took them to complete the pre-training procedure.

Visual discrimination training

A session began with the delivery of a food pellet, activation of the house and reward light, as well as the sounding of a short tone (0.5sec). Once the rodent collected the pellet, two images would be displayed in two of four locations upon the screen. The location of these images varied from trial to trial. A response at the "correct" image, the image associated with reward for the rodent, would result in the delivery of a food pellet reward, the sounding of the reward tone, and activation of the magazine light. Once this pellet was collected, the reward light would turn off and the inter-trial interval would begin (ITI). The ITI lasted for 10secs and at the end of this time period the magazine light would again turn on, indicating that the rat must nose poke in order to start the next trial. A nose poke at the reward magazine would cause the light in the magazine to turn off and would trigger the start of the next trial, along with the display of the stimuli upon the screen. If however an animal selected the "incorrect" stimuli, the image not associated with reward, then the images would be removed from screen and a short "punishment" period would begin. During this time period the house light would turn off (10sec) and at the end of the period the ITI would begin. A correction trial procedure was used, meaning that rats would be presented with the same trial until a correct response was made. However correction trials did not count towards the total number of trials, nor were they included in accuracy or response latency calculations. A trial stopped after either 45mins or the completion of 60 trials.

Study 1a, 1b

At the start of testing equal number of animals were assigned to either the "part" or "whole" condition (see figure 2a, b) as previously described Rate of acquisition between the two groups was then compared. Repeated measure ANOVA's, with "session" as the repeated measure, were used to compare the rate of acquisition between groups. Animals were trained for 22 sessions in experiment 1a, and 23 sessions in experiment 2a. We hypothesized that animals might display a configural superiority effect if they had already been trained to recognise the orientation (meaningful information) of the stimulus. Accordingly at the end of the acquisition phase of the study those animals that had been trained on the "part" stimuli were placed on the comparable "whole" stimuli for half of their 60 daily sessions, while still be tested on the their previously acquired "part" stimuli. Animals were tested under this condition for an additional 13 sessions (experiments 1b)
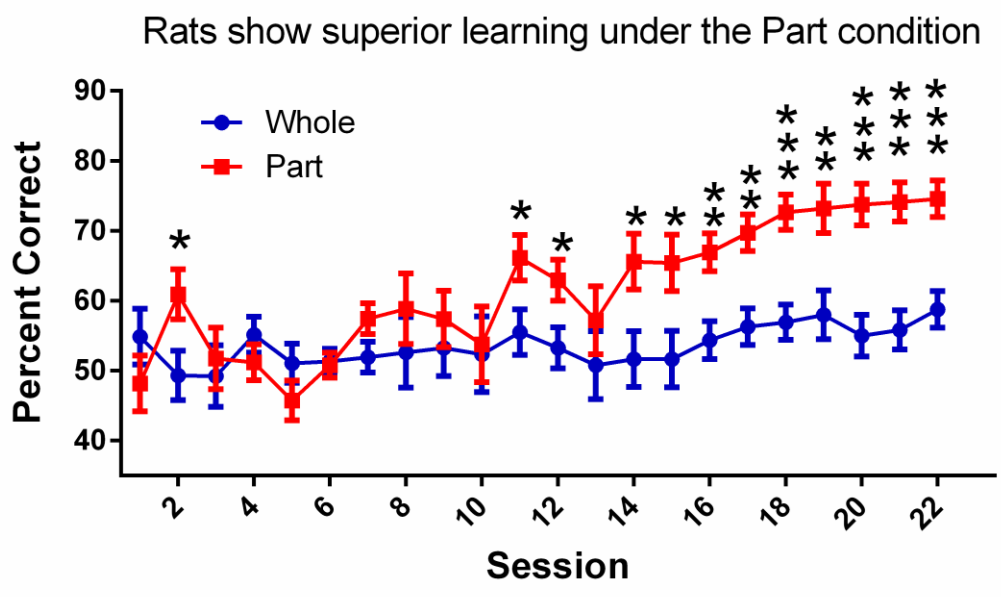
Study 2a,b

The training used here was identical to that employed in study 1, except for the fact that new stimuli were used, and animals were trained for 23 days in experiment 2a. Moreover a new cohort of 24 rats was used for this phase of the study. As in experiment 1, we hypothesized that animals might display a configural superiority effect if they had already been trained to recognise the orientation (meaningful information) of the stimulus. Accordingly at the end of each acquisition study those animals that had been trained on the "part" stimuli were placed on the comparable "whole" stimuli. Unlike in experiment 1b animals were only presented with "whole" stimuli.

Previous experince with Part stimuli does not facilitate performance on whole stimuli
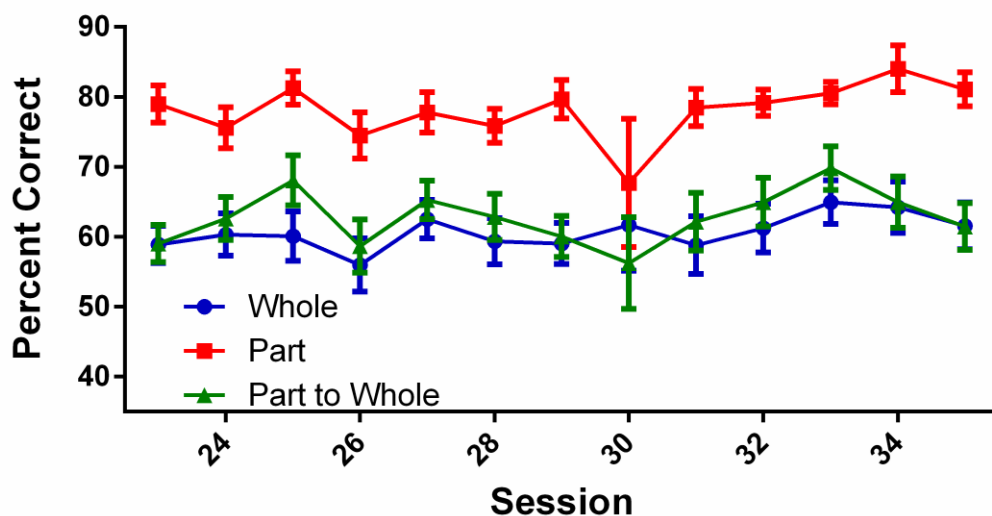
Results

Statistical analysis,

Repeated measure ANOVAs were used throughout this study where "session" served as the repeated measure and stimuli type as the dependent variable. T-tests were used to determine differences between groups on specific testing days, or in situations where a lack of variance prevented the use of an ANOVA. The primary measure within this study was percent correct (correct trials/total trials completed). Response latencies (interval from the onset of the stimuli to a response) and collection latencies (time from a correct response at the screen to pellet collection) were also collected (log10 ms). A log10 transformation was performed on response and collection latency to normalize the skewed distribution that often occurs with timed data.

Experiment 1a,

After 22 sessions of testing there was a clear effect of stimulus type on percent correct responses (F(1,22)=13.796), P=0.001) with animals learning the "part" stimuli at a faster pace. Moreover a clear interaction between stimulus type and session was seen (F(21, 462)=2.819; P<0.001; Figure 2a).

Stimulus type also had a significant effect on response latency, with the "whole" group responding to the onset of stimuli significantly faster (F(1,22)=5.26, P=0.031) then those animals trained to respond to "part". Yet, no interaction between session and stimulus type was observed (F(21, 462)=1.42, P=0.10), despite a main effect of session on response latency (F(21, 462)=48.11, P<0.001; Table 1). Animals trained under the whole condition were also slightly faster to collect their reward pellet (F(1, 21)=4.441, P=0.049), and all animals became faster with training (F(1, 21)=4.81, P<0.001). However session and stimulus

type did not interact (F(21, 399)=1.17, P=0.27). The significantly faster responses of the rodents in the whole condition might suggest that the rats are showing some kind of advantage for this condition; however it should be kept in mind that the average accuracy of the rats in this condition remains around 50% over the course of experiment 1. Indeed using a binomial test, none of the rats in the whole condition show above chance performance.

Owing to a lack of variance in the dataset, a within subject ANOVA could not be used to examine the effects of stimulus type on trials completed. Accordingly a way-one ANOVA was used to examine the effects of stimulus type on cumulative errors. Accordingly stimulus type ("whole" versus "part" did not influence total trials completed (F(1, 22)=1.581, P=0.22; Table 1).

Experiment 1b,

After 22 sessions of training, the rats who had learned to discriminate the "part" stimuli where tested on their ability to discriminate between the stimuli in the "whole" condition. This was done to determine if after learning to discriminate under the "part" condition this discrimination could be enhanced by the introduction of the additional information contained within the "whole" condition. When animals initially trained on just the "part" condition were tested on both stimuli types within a single session animals were again significantly more accurate when discriminating the "part" rather than the "whole" condition (F(1, 22)=19.02), P>0.001; Figure 2b). Moreover no interaction was detected between session and stimulus type suggesting that no further learning occurred (F(12, 264)=0.55, P=0.88). This was supported by a Dunnetts t-test showing no difference from accuracy on the first session of testing with the new stimulus and all additional days. Interestingly animals performed significantly "above chance" on all but one session with the "whole" stimuli (session 8). This suggests that some generalization from the "part" condition to the "whole" condition did occur.

Experiment 2a,

As in experiment 1a animals trained on "part" stimuli acquired the task quicker than those animals trained to discriminate the "whole" stimuli (F(1, 22)=15.465, P<0.001; Figure 3a). Session was also found to interact with stimulus type (F(22, 484)=4.488, P<0.001). In this instance no difference was seen as a result of stimulus type on response latency(F(1,22)=1.72, P=0.22). Nor did an interaction exist between session and stimulus type (F(22, 484)=0.79, P=0.74), while animals did respond faster across testing sessions (F(1,22)=11.82, P<0.001). Animals trained under the whole stimuli condition were significantly faster to collect a reward pellet (F(1, 22)=4.0, P=0.036), and all animals did become faster with training (F(1, 22)=10.4, P<0.001). However there was no interaction between training and stimuli type (F(22, 484)=1.1, P=0.37; Table 1).

Experiment 1A

	Response Latency (Log10 msec)				Collection Latency (Log10 msec)				Percent Trials Completed			
	Part		Whole		Part		Whole		Part		Whole	
Session	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
1	4.07	0.035	4.018	0.035	3.415	0.105	3.487	0.1	47.2	5.9	48.3	6.2
2	3.992	0.047	3.929	0.047	3.593	0.089	3.373	0.085	37.5	8.1	44.9	5.4
3	3.97	0.044	3.921	0.044	3.505	0.087	3.335	0.083	24.9	6.3	41.9	7.9
4	3.913	0.041	3.779	0.041	3.487	0.065	3.345	0.062	49.2	6	73.6	7.9
5	3.884	0.038	3.718	0.038	3.44	0.069	3.369	0.066	49.6	8.9	81	6
6	3.795	0.04	3.612	0.04	3.496	0.078	3.306	0.075	60.7	9.6	80.3	9.3
7	3.762	0.041	3.632	0.041	3.356	0.038	3.331	0.036	66.8	9.4	87.9	8.3

| Session	Part Mean	Part SEM	Whole Mean	Whole SEM	Part Mean	Part SEM	Whole Mean	Whole SEM	Part Mean	Part SEM	Whole Mean	Whole SEM
8	3.743	0.041	3.615	0.041	3.387	0.056	3.295	0.054	71.4	12.1	92.2	7.8
9	3.71	0.042	3.606	0.042	3.327	0.016	3.28	0.015	75.8	10.3	91.4	7
10	3.645	0.04	3.63	0.04	3.356	0.033	3.301	0.031	89.9	8.2	92.1	7.9
11	3.722	0.043	3.549	0.043	3.334	0.03	3.303	0.028	91.5	7.6	89.7	8.2
12	3.681	0.039	3.568	0.039	3.295	0.019	3.273	0.018	91.9	8.1	92.2	7.6
13	3.652	0.031	3.564	0.031	3.329	0.037	3.349	0.036	84	10.8	90.1	8
14	3.666	0.031	3.567	0.031	3.288	0.021	3.285	0.02	96.1	3.9	91.9	8.1
15	3.633	0.042	3.573	0.042	3.261	0.031	3.283	0.029	100	0	91.8	8.2
16	3.601	0.039	3.531	0.039	3.307	0.037	3.258	0.035	100	0	97.1	2.9
17	3.565	0.041	3.568	0.041	3.273	0.024	3.23	0.023	100	0	99.9	0.1
18	3.592	0.038	3.549	0.038	3.256	0.017	3.229	0.016	100	0	100	0
19	3.616	0.045	3.548	0.045	3.288	0.022	3.238	0.021	98.2	1.8	99.9	0.1
20	3.626	0.04	3.543	0.04	3.286	0.025	3.285	0.024	100	0	100	0
21	3.577	0.032	3.525	0.032	3.259	0.018	3.224	0.018	99.9	0.1	100	0
22	3.571	0.032	3.513	0.032	3.288	0.019	3.224	0.018	100	0	100	0

Experiment 2A

	Response Latency (Log10 msec)				Collection Latency (Log10 msec)				Percent Trials Completed			
	Part		Whole		Part		Whole		Part		Whole	
Session	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
1	3.603	0.028	3.532	0.028	3.305	0.025	3.265	0.025	79.9	8.6	92.4	4
2	3.596	0.052	3.586	0.052	3.371	0.061	3.247	0.061	72.5	12	93.3	6.1
3	3.548	0.029	3.509	0.029	3.295	0.033	3.222	0.033	81.7	9.2	95.3	3.3
4	3.547	0.030	3.450	0.030	3.294	0.03	3.215	0.03	84.4	8.3	96.7	3.2
5	3.538	0.026	3.501	0.026	3.264	0.016	3.195	0.016	90.5	9.1	100	0
6	3.503	0.027	3.500	0.027	3.253	0.018	3.186	0.018	83.3	11.2	100	0
7	3.456	0.024	3.437	0.024	3.235	0.017	3.185	0.017	100	0	100	0
8	3.491	0.025	3.481	0.025	3.218	0.015	3.172	0.015	100	0	98.9	1.1
9	3.498	0.033	3.454	0.033	3.221	0.017	3.171	0.017	82.2	7.6	78.9	9.8
10	3.421	0.022	3.429	0.022	3.198	0.015	3.156	0.015	88.5	6.5	99.9	0.1
11	3.455	0.026	3.402	0.026	3.176	0.016	3.168	0.016	99.9	0.1	100	0
12	3.461	0.025	3.414	0.025	3.202	0.017	3.169	0.017	100	0	100	0
13	3.468	0.025	3.420	0.025	3.193	0.015	3.17	0.015	99	1	100	0
14	3.466	0.026	3.457	0.026	3.227	0.02	3.187	0.02	100	0	100	0
15	3.442	0.024	3.439	0.024	3.197	0.016	3.17	0.016	100	0	100	0
16	3.507	0.020	3.454	0.020	3.188	0.017	3.17	0.017	100	0	100	0
17	3.484	0.018	3.434	0.018	3.181	0.017	3.16	0.017	100	0	98.8	1.3
18	3.455	0.022	3.427	0.022	3.182	0.019	3.181	0.019	100	0	97.1	2
19	3.473	0.025	3.436	0.025	3.188	0.016	3.155	0.016	100	0	100	0
20	3.467	0.023	3.434	0.023	3.183	0.015	3.167	0.015	100	0	100	0
21	3.452	0.020	3.417	0.020	3.167	0.015	3.142	0.015	100	0	100	0
22	3.433	0.018	3.400	0.018	3.162	0.017	3.126	0.017	97.5	2.5	99.9	0.1
23	3.440	0.024	3.389	0.024	3.166	0.018	3.144	0.018	100	0	100	0

Table 1,
Summary of secondary variables from Experiments 1a and 2a.

Owing to a lack of variance a one-way ANOVA was used to determine the impact of stimulus type on trials completed. Stimulus type had a small but significant impact on trials completed, with the "whole" group completing more trials on average $(F_{(1,22)}=5.45, P=0.029;$ Table 1).

Previous experince with Part stimuli does not facilitate performance on whole stimuli
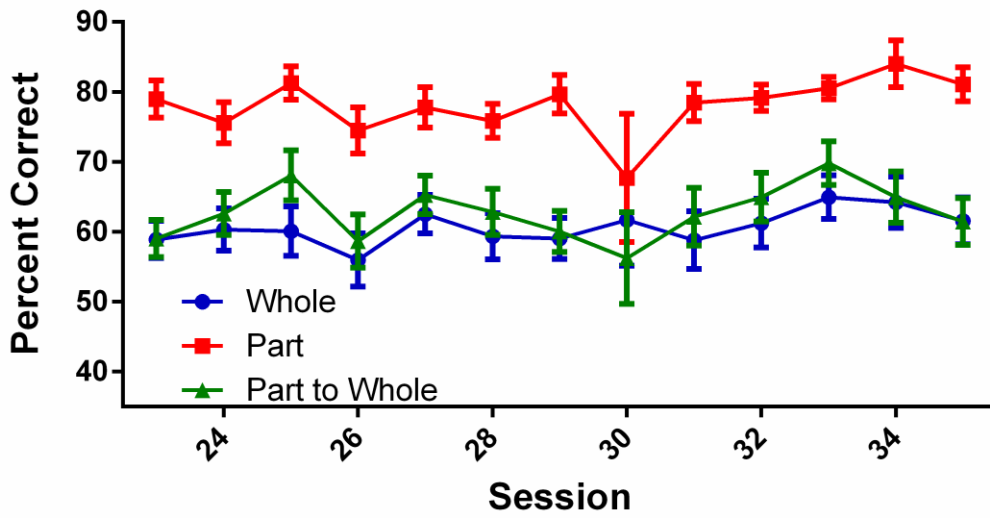
Experiment 2b,

Once animals had acquired the "part" stimuli they were switched to "whole" stimuli. Animals clearly performed worse than on the final day of testing (P<0.001), although they responded significantly above chance performance level (day 24 P=0.047, Day 25 P=0.005).

Previous experince with Part stimuli does not facilitate performance on whole stimuli
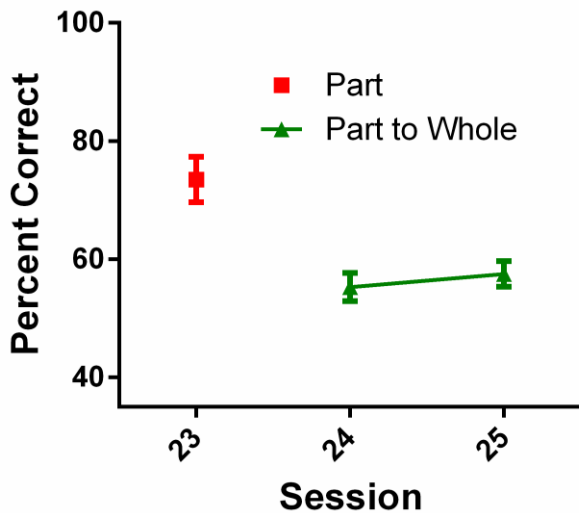
Discussion

The results of experiment 1a clearly provide no support for the existence of a configural superiority effect in the rat. It should be noted previous research has however highlighted that rats sometimes solve visual discriminations by basing their choice on just a portion of the stimuli as opposed to the whole image (Minini & Jeffery, 2006). In order to further test that the lack of an advantage for configural stimuli was not the result of an idiocyncratic feature of the exact size and nature of the stimuli used in experiment 1, we sought to replicate the effect using an array of stimuli, with a jittered position. As observed in experiments 1A, B, rats learned to discriminate the "part" stimuli faster than they learned to discriminate "whole" stimuli. In fact, rats actually show a clear advantage in the accuracy of their responses in the "part" condition, counter to what is observed in humans. Rats did perform slightly faster in the whole condition, but given that their performance remained close to chance across the experiment, it is most likely that this difference in reaction time reflects additional time spent selecting the correct option in the "part" condition, rather than a genuine advantage for the whole condition (e.g. scanning stimuli, and "switching" selection if the stimulus initially selected would be incorrect). In experiments 2a and 2b no improvement in performance was observed in those animals that had originally been trained on the "part" discrimination, but were then tested under the "whole" condition. These findings further suggest that rats do not display a configural superiority effect.

In humans, the addition of non-informative input can improve the speed and accuracy of a visual discrimination. This illustrates that in human vision we sometimes perceive a "Gestalt" or whole, which is different to the sum of its parts. There is increasing evidence that the primacy of Gestalts in human perception reflects the dominance of the more abstract representations developed in the further stages of the complex hierarchy of areas in the human visual system (Hochstein & Ahissar, 2002). However, so far it was unclear if this phenomenon exists in the simpler visual system of the rodent. Accordingly we used touchscreen technology to compare the performance of animals trained to discriminate "whole" or "part" stimuli similar to those used by Pomerantz et al. (1977). Rodents showed no evidence of enhanced learning when presented with a configuration of edges that elicits a Gestalt in humans. In fact the opposite effect was seen, animals actually performed much worse, indicating that the "non-informative" input was more than just redundant, but actually served to obfuscate the critical information needed to solve the task. Moreover, when animals had learned the discrimination that consisted of just lines differing in their orientation (Parts), they were also impaired when switched to the configuration of edges (whole stimuli). Interestingly this pattern of performance is qualitatively similar to that seen in Pigeons (Kelly & Cook, 2003), New World Monkeys (Neiworth *et al.*, 2014) and a severe visual form agnosia patient who suffered damage to higher areas of the ventral visual stream (de-Wit *et al.*, 2012). This qualitative similarity could suggest that rodents lack some of the higher visual areas that might be necessary for this Configural Superiority Effect (Kubilius *et al.*, 2011). While it is possible that the effect observed here could be partly dependent upon the strain of rat used, we have no reason to believe this to be the case, and

it has been demonstrated that Lister-Hooded rats will outperform several other strains of rats on acquisition of a visual discrimination (Kumar *et al.*, 2015).

An important difference in the experimental design used here, and that in the original work by Pomerantz et al. (1977) is that here we were measuring rate of learning as our primary endpoint for evidence of a Configural Superority Effect that occurred over days. In contrast, Pomerantz and colleagues used an oddity detection task that would not have required learning. Accordingly, these two tasks will likely differ in non-perceptual cognitive demands. Unfortunately there is no evidence to support that rodents can perform an oddity detection task using *2 dimensional* visual stimuli. Similarly rodents have not been able to perform non-match to sample tasks using a non-spatial image in a touch-screen environment. Accordingly at this time it is impossible to fully replicate the procedure used by Pomerantz in the rodent. However in an attempt to control for these potential differences in learning and memory we performed experiments 1B and 2B, where once animals had learned to discriminate based on "part" stimuli they were exposed to the corresponding "whole" images. This condition should remove most of the "learning" element from the task, resulting in a situation with cognitive demands that more greatly resemble those used by Pomerantz et al. (1977) as learning was not required. However the addition of this extra information did not facilitate performance, and in fact, in line with the results of 1A and 1B disrupted performance. Accordingly we are inclined to believe that differences in task requirements are not the root cause for a lack of a Configural Superiority Effect in rodents.

As of yet we see no evidence for the configural superiority phenomenon and the fact that an impairment was observed suggests that rodents are heavily biased towards using local cues rather than global "Gestalts" when processing visual stimuli. While the phenomena of configural superiority may still exist in the rat, these data suggest that if it does exist it may be qualitatively different from the phenomena observed in humans. This highlights a limitation in the extent to which the rodent can be used to model human visual perception, and important finding for pre-clinical translational *vivo* scientists, although the may still serve as a valuable tool for studying other aspects of visual perception.

It is possible that a Configural Superiority effect may have been detected if different stimuli sets had been used. However we selected to focus our efforts on this specific set of images as they showed one of the most robust responses in the original human study performed by Pomerantz et al. (1977). Moreover we used stimuli of different sizes to ensure that the observed results were not size dependent. While the weight of evidence against a Configural Superiority effect could have been increased with the use of additional stimuli this would have required the sacrifice of a tremendous number of animals. In our experience animals that have been placed on a visual discrimination, but fail to learn because of overly difficult stimuli will struggle or fail to learn later discriminations with "easier" stimuli. Presumably this is because the visual discriminations becomes a fixed ratio 2 task and the animal stops attending to the stimulus prior to the response. According it would have been necessary to use a new group of animals for every condition tested. This

would be experimentally difficult and ethically questionable considering the conclusions from studies 1 and 2. However if rodents could be trained to perform a spontaneous visual oddity task then it would be possible to test a greater number of visual stimuli and more conclusively demonstrate a lack of Configural Superiority Effect in rodents. However seeing the time it takes for rodents to learn a basic visual discrimination such a task may be beyond their abilities. These data suggest that any configural superiority effect displayed in rodents will be different then that seen in humans. However additional work with different stimuli and other strains or rodents would be necessary to more completely rule out the general phenomena in the rodent.

While this research highlights the potential limits of the rodent as a pre-clinical model for the human visual system, it further points to the importance of cross species comparisons of perceptual phenomenon evident in human vision. Taken at face value, the current result suggests that only species most closely related to humans (that is old world primates) show a clear configural superiority effect (Neiworth *et al.*, 2014). Again however this pattern of results should be viewed as an inspiration to further research rather than offering a definitive conclusion. In particular there is evidence that even simpler visual systems, like those of the Bee, are sensitive to complex visual shape representations (Chen *et al.*, 2003) that might be sufficient to cause a Configural Superiority Effect. This is however an important unknown, and we hope the current research acts as a catalyst to further cross-species comparisons that could help us to further understand under what conditions wholes become more than the sum of their parts.

Bussey, T.J., Padain, T.L., Skillings, E.A., Winters, B.D., Morton, A.J. & Saksida, L.M. (2008) The touchscreen cognitive testing method for rodents: how to get the best out of your rat. *Learn Mem*, **15**, 516-523.

Butler, P.D., Silverstein, S.M. & Dakin, S.C. (2008) Visual perception and its impairment in schizophrenia. *Biol Psychiatry*, **64**, 40-47.

Chen, L., Zhang, S. & Srinivasan, M.V. (2003) Global perception in small brains: topological pattern recognition in honey bees. *Proc Natl Acad Sci U S A*, **100**, 6884-6889.

de-Wit, L.H., Kubilius, J., Wagemans, J. & Op de Beeck, H.P. (2012) Bistable Gestalts reduce activity in the whole of V1, not just the retinotopically predicted parts. *J Vis*, **12**.

Fellini, L., Kumar, G., Gibbs, S., Steckler, T. & Talpos, J. (2014) Re-evaluating the PCP challenge as a pre-clinical model of impaired cognitive flexibility in schizophrenia. *Eur Neuropsychopharmacol*, **24**, 1836-1849.

Hochstein, S. & Ahissar, M. (2002) View from the top: hierarchies and reverse hierarchies in the visual system. *Neuron*, **36**, 791-804.

Hubel, D.H. & Wiesel, T.N. (2009) Republication of The Journal of Physiology (1959) 148, 574-591: Receptive fields of single neurones in the cat's striate cortex. 1959. *J Physiol*, **587**, 2721-2732.

Kelly, D.M. & Cook, R.G. (2003) Differential effects of visual context on pattern discrimination by pigeons (Columba livia) and humans (Homo sapiens). *J Comp Psychol*, **117**, 200-208.

Kirby, E., Bandelow, S. & Hogervorst, E. (2010) Visual impairment in Alzheimer's disease: a critical review. *J Alzheimers Dis*, **21**, 15-34.

Kubilius, J., Wagemans, J. & Op de Beeck, H.P. (2011) Emergence of perceptual Gestalts in the human visual cortex: the case of the configural-superiority effect. *Psychol Sci*, **22**, 1296-1303.

Kumar, G., Talpos, J. & Steckler, T. (2015) Strain-dependent effects on acquisition and reversal of visual and spatial tasks in a rat touchscreen battery of cognition. *Physiol Behav*, **144**, 26-36.

Lamme, V.A. (1995) The neurophysiology of figure-ground segregation in primary visual cortex. *J Neurosci*, **15**, 1605-1615.

Minini, L. & Jeffery, K.J. (2006) Do rats use shape to solve "shape discriminations"? *Learn Mem*, **13**, 287-297.

Neiworth, J.J., Whillock, K.M., Kim, S.H., Greenberg, J.R., Jones, K.B., Patel, A.R., Steefel-Moore, D.L., Shaw, A.J., Rupert, D.D., Gauer, J.L. & Kudura, A.G. (2014) Gestalt principle use in college

students, children with autism, toddlers (Homo sapiens), and cotton top tamarins (Saguinus oedipus). *J Comp Psychol*, **128**, 188-198.

Pasupathy, A. & Connor, C.E. (2002) Population coding of shape in area V4. *Nat Neurosci*, **5**, 1332-1338.

Pomerantz, J.R., Sager, L.C. & Stoever, R.J. (1977) Perception of wholes and of their component parts: some configural superiority effects. *J Exp Psychol Hum Percept Perform*, **3**, 422-435.

Robertson, C.E., Thomas, C., Kravitz, D.J., Wallace, G.L., Baron-Cohen, S., Martin, A. & Baker, C.I. (2014) Global motion perception deficits in autism are reflected as early as primary visual cortex. *Brain*, **137**, 2588-2599.

Skottun, B.C., De Valois, R.L., Grosof, D.H., Movshon, J.A., Albrecht, D.G. & Bonds, A.B. (1991) Classifying simple and complex cells on the basis of response modulation. *Vision Res*, **31**, 1079-1086.

Wagemans, J., Elder, J.H., Kubovy, M., Palmer, S.E., Peterson, M.A., Singh, M. & von der Heydt, R. (2012) A century of Gestalt psychology in visual perception: I. Perceptual grouping and figure-ground organization. *Psychol Bull*, **138**, 1172-1217.

Wertheimer, P., de, R., Descotes, J., George, P. & Gerin, M. (1961) [Experimental data relative to selective deep hypothermia of the brain]. *Lyon Chir*, **57**, 222-228.