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Do gorillas (*Gorilla gorilla*) and orangutans (*Pongo pygmaeus*) fail to represent objects in the context of cohesion violations?

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ABSTRACT

Recent research suggests that witnessing events of fission (e.g., the splitting of a solid object) impairs human infants', human adults', and non-human primates' object representations. The present studies investigated the reactions of gorillas and orangutans to cohesion violation across different types of fission events implementing a behavioral paradigm previously used with human infants. Results suggest that fission events vary in their impact on representational abilities but do not destroy apes' representations of continuously existing objects.

1. Introduction

What enables infants to represent objects as distinct individuals persisting through space and time? According to the *core knowledge approach* (e.g., Spelke, 1994, 2000; Spelke, Breinlinger, Macomber, & Jacobson, 1992; Spelke & Kinzler, 2007) infants perceive the unity and boundaries of objects based on spatiotemporal information operating on three principles inherent in perceived motion (Spelke, 1990, 1994, 2000): (a) cohesion (objects are connected bounded units), (b) continuity (objects are solid entities that continuously exist in space and time), and (c) contact (objects move together or affect one another's motion only if they touch). These principles are crucial for perceiving as well as for representing and reasoning about objects because they capture the essence of and provide criteria for *objecthood*.

1.1. Cohesion defines objecthood

Cohesion is proposed to be the most powerful principle defining the ontological category of objects (Bloom, 2000; Pinker, 1997; Scholl, 2007). Obviously perceived cohesion (or "psychological cohesion") is not congruent with physical cohesion (i.e., the coherence of atoms and molecules of a physical body or fluid), and the cohesive forces as described in physics are not directly accessible by visual perception. In psychological terms, cohesion is exemplified by the presence of surface points and their spatiotemporal relations in the field of vision. Two key features are proposed to be at the roots of infants' inferences about object cohesion (Spelke, 1990, 1994): connectedness (perceived contact between surface points) and boundedness (rigidity of contour).

Recently, several studies have tried to determine how cohesion constitutes object representations by confronting human infants and adults with cohesion violations (Cheries, Mitroff, Wynn, & Scholl, 2008; Chiang & Wynn, 2000; Huntley-Fenner, Carey, & Solimando, 2002; Mitroff, Scholl, & Wynn, 2004; Rosenberg & Carey, 2006; vanMarle & Scholl, 2003). The rationale behind these investigations

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is that if perceived cohesion constitutes the ability to represent, track, and reason about persisting objects, this ability should be affected by the violation of this core principle. Reactions to cohesion violations were investigated in two types of situations: (a) the contrasting of solid objects with non-solid substances[1] and (b) events of fission (i.e., the splitting of a solid object).

1.2. Non-solid substances

The ontological distinction between objects and substances is basic and already available to very young children in their lexical development. Children are biased to interpret novel words used to refer to cohesive entities as names for objects and novel words used to refer to non-cohesive entities as names for materials (Hall, 1996; Imai & Gentner, 1997; Samuelson & Smith, 1999; Soja, 1992; Soja, Carey, & Spelke, 1991, 1992). In contrast to solid objects, children conceive of materials ("matter"[2]) as having an arbitrary structure (Prasada, Ferenz, & Haskell, 2002). Non-solid substances are an extreme example of an entity completely lacking structural stability and thus cohesiveness (connectedness and boundedness). In contrast to solid (rigid) objects, non-solid substances should therefore not be represented as continuously existing entities.

Huntley-Fenner et al. (2002) found that 8-month-old infants fail to represent the continuous existence of sand piles. These results were confirmed by Rosenberg and Carey (2006), who report that infants fail to trace piles of sand. In contrast, adults may encode non-cohesive materials either as an individuated entity (pile, portion) or an un-individuated entity (sand). However, research on adult perception demonstrated that also adults fail to track non-solid "pouring", the crucial factor impairing adults tracking abilities being the substance-like non-rigid motion with dynamic extension and contraction (vanMarle & Scholl, 2003).

1.3. Fission

The above mentioned studies deal with highly salient forms of cohesion violations because they present non-solid, non-cohesive substances and thus entities that do not belong to the domain of the core system of solid physical objects. Therefore investigations that examine the effects of cohesion violations on an already established object representation, (i.e., when witnessing the fission or decomposition of solid objects) are of special interest. Problems of fission challenge our intuitions about objects because they violate the core principles defining what counts as an object (Scholl, 2007). What happens to the original object when it breaks into two parts? Is either of the resulting halves now congruent with the initial object, or does – in our experience – the object even cease to exist? Chiang and Wynn (2000) compared 8-month-old infants' reasoning about solid objects and collections of objects such as non-cohesive piles of objects (pyramids of blocks) in occlusion events. When infants were presented with solid pyramids that maintained their boundaries throughout the whole event, they succeeded in this task. However, if infants first saw the decomposition of the pyramid into five blocks and then their rearrangement into a pyramid, they failed to track and individuate the objects. This is highly remarkable because it suggests that infants' ability to represent objects is directly affected by cohesion violations (i.e., by the decomposition of an object in its parts). Chiang and Wynn (2000) offered two explanations why infants' object representations do not survive the cohesion violation. First, infants may fail to represent the continuous existence of a non-cohesive collection because they conceive of it as of a *non-object* entity. Even though infants might be able to construe collections as individual entities, they may be aware that they must not obey the principles that constrain solid objects (i.e., flocks of birds, swarms of fishes do not maintain boundaries [cohesion], may pass each other [solidity], and may even temporarily cease to exist [continuity]). A second possibility is that infants' object-tracking mechanisms are disrupted by cohesion violations. For example, infants may have failed to track an object decomposed into parts due to the resulting spatial ambiguity (i.e., the inability to address multiple spatial locations by a single "object-file").

Cheries et al. (2008) showed that even the most simple cohesion violation, the fission of a single solid object into two parts affects infants' ability to represent and quantify objects. They adopted a crawling paradigm previously used by Feigenson, Carey, and Hauser (2002) to test infants' ability to represent relative quantities. Infants were presented with two conditions: a split condition and a no-split condition. In the no-split condition, 10- to 12-months-old infants saw one cracker being lowered into a cup and two crackers placed into another cup. They consistently selected the cup with the greater amount of cracker. However, if infants were first presented with a single big cracker that was split into two halves before placing it into the cup, infants failed to have an above-chance preference for either cup, even though the quantities to compare were exactly the same in both conditions. This effect had disappeared by the age of 16 months (Cheries & Carey, 2009). The authors concluded that witnessing the cohesion violation (i.e., the splitting manipulation) affected the younger infants' object representation, and thus they failed to quantify the crackers. Like Chiang and Wynn (2000), they suggested that infants' object representation could have been completely destroyed by observing the cohesion violation. In addition, they raised the possibility that the initial representation survived the splitting but was impaired and thus ineffective in comparative judgments. This is exactly what was observed in adults. Objects smoothly splitting into two parts highly limited adults' object-tracking mechanisms (Mitroff et al., 2004). However, even though adults' object representations were heavily affected in their functionality, they clearly survived the

[1] In developmental research on non-solid substances, the term *non-solid* does not refer to physical conditions of aggregation (solid, fluid, gaseous) but refers to the criterion of *deformability*. Thus, for example, sand is not considered a solid (as in physics) but a non-solid substance.

[2] In principle (and following Aristotle's use of the term, see Prasada, 1999) the ontological category of "matter" is composed of both solid (e.g., wood) and non-solid substances (e.g., sand). However, in the recent infant research presented here (adjusted to their respective research purposes) the term *substance* is used to refer to non-solid substances only.

splitting. A similar pattern also emerged in research on non-human primates.

1.4. Knowledge about cohesion in non-human primates

One of the central tenets of the core knowledge thesis (e.g. Spelke, 1994; Spelke & Kinzler, 2007) is that basic cognitive mechanisms are innate and have a long phylogenetic history. This means that they are universal in humans and shared with other primate species. If this hypothesis is true, we would expect that core knowledge is also present in a wide range of non-human primate species, particularly with those that are closely related to humans. Core principles such as cohesion serve to represent and reason about particular kinds of ecologically important events and entities. In fact, the principle of cohesion may be one of the most crucial principles for defining and representing objects. Moreover, it is conceivable that the cohesion principle, just like other aspects of core knowledge, is likely to be present in a variety of non-human primate species (e.g., Cacchione & Call, 2010; Cacchione, Call, & Zingg, 2009; Cacchione & Krist, 2004; Feigenson, Dehaene, & Spelke, 2004; Hauser & Carey, 2003; Mendes, Rakoczy, & Call, 2008; Santos, 2004; Spelke, 2000, 2004).

Despite its theoretical importance, few studies have investigated whether the cohesion principle plays a key role in the way that non-human primates represent objects. Munakata, Santos, O'Reilly, Hauser, and Spelke (2001) reported that rhesus macaques (*Macaca mulatta*) expect objects to retain cohesive boundaries as they move. vanMarle, Aw, McCrink, and Santos (2006) found that capuchins (*Cebus apella*) equally well enumerated sets of solid (raisins) and non-solid entities (scoops of banana puree). Similarly, Wood, Glynn, Hauser, and Barner (2008) reported that rhesus macaques are able to enumerate "pours" of carrot pieces. Apparently, rhesus monkeys (like human adults) manage to encode non-cohesive materials as distinct entities using a salient criterion (such as a distinct number of "scoops" or "pours"). However, Mahajan, Barnes, Blanco, and Santos (2009) recently found that brown lemurs (*Eulemur fulvus*) fail to quantify non-solid substances in the absence of such criteria. Like infants, brown lemurs successfully enumerated rigid cohesive objects but failed to do so in case of piles of sand. But in contrast to 10- to 12-months-old human infants, lemurs successfully enumerated objects that were decomposed into multiple pieces. Thus, their performance resembled that of 16-months-old human infants and adults.

In sum, the present state of research studies suggests (a) that cohesion violations may impair human infants', human adults', and non-human primates' ability to represent, individuate, and track objects, (b) that observed reactions to cohesion violations are stronger for non-solid substances (and thus non-object entities) than solid objects (i.e. fission events), and (c) that at least the vulnerability to fission-type cohesion violations follows a developmental trend. These results are of great theoretical relevance because they suggest that these abilities root in the same cognitive mechanisms (Carey & Xu, 2001; Leslie, Xu, Tremoulet, & Scholl, 1998) and that inferences about the persistence and identity of objects are based on a domain-specific body of knowledge about discrete, bounded, cohesive physical bodies and rule out low-level perceptual accounts, which would equally refer to all kinds of visual features (e.g., Bogartz, Shinksey, & Schilling, 2000; Bogartz, Shinksey, & Speaker, 1997; Cashon & Cohen, 2000; Haith, 1998; Meltzoff & Moore, 1998).

1.5. The present studies

The present research focuses on great apes' reactions to fission events (i.e., events in which a solid object is decomposed into multiple parts). Although previous work on lemurs has suggested the operation of the cohesion principle, this species is only distantly related to humans. Inferring a shared cognitive mechanism based on a pair of distantly related species is problematic because humans and lemurs may have evolved their abilities independently not by inheriting them from their common ancestor. Moreover, data on multiple species are required to be able to make strong inferences about the distribution and evolution of cognitive abilities. Furthermore, if human cognition is the focus of interest, data on species closely related to humans, such as orangutans and gorillas, are particularly important.

Consequently, a first goal of the present study was to verify that gorillas and orangutans manage to represent and quantify split objects as suggested by Mahajan et al. (2009). We aimed to complete the picture sketched by Mahajan et al. (2009) in two respects: first, by using action-based measures (not a perception-based method as was used by Mahajan and colleagues) which allows for a direct comparison with the original human infant study of Cheries et al. (2008); and second, by adding important great ape data to confirm the pattern suggested by Mahajan et al. (2009). Indeed, detecting the cohesion principle at work in great apes would strengthen the hypothesis that knowledge about cohesion, just like other aspects of core knowledge, has a long evolutionary history and may ultimately be traced down to a common ancestor of all primate species living today (e.g., Feigenson et al., 2004; Spelke, 2000, 2004).

Another goal of the present research was to determine how the probability that apes succeed in representing and quantifying split objects varies as a function of the type of fission presented. A split into two identical halves (as presented by Cheries and colleagues and Mahajan and colleagues) is only one of many conceivable splitting events, which may vary in their impact on apes' ability to represent an object's continuous existence. Imagine a fission event in which an object is split into two (Fig. 1).

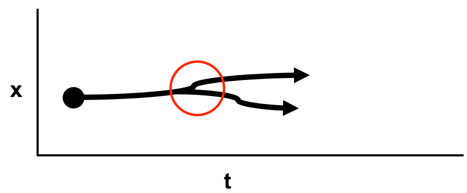

Fig. 1. Schematic depiction of a fission event and its impact on an objects' spatiotemporal path.

The bifurcation highlighted with a circle marks the moment where the representation is interrupted, most likely caused by the impossibility to decide which of the two resulting parts should now be addressed as the "original object". It seems likely that this decision varies across variants of fission events. First of all, it may depend on the number and type of resulting elements. For example, it may be easier to maintain a stable object representation if only a small part of the original object is broken off, or more difficult if it is broken in many small pieces.

Second, the temporal structure of the original objects' disassembly may be of relevance. For example, object representations may be more affected if the disassembly occurs in one moment than when an object erodes slowly and successively. Finally, variants of fission events may vary in their impact on the elements of perceived cohesion (*connectedness*: perceived contact between surface points; and *boundedness*: rigidity of contour). For example, object representations may be less affected by fission events that preserve an objects' outer contour.

A final goal was to find out more about how cohesion violations affect the ability to maintain stable and functional object representations. Up to now, it is unclear why young infants failed to represent the continuous existence of objects in splitting events. Were their representations fully destroyed or simply limited in their functions (as was observed in adults)? To be able to interpret a potential representational breakdown in apes, we presented them with task conditions varying in complexity. Previous research suggests that tasks involving a larger proportionate difference (i.e., a small ratio defined as the smaller quantity divided by the larger quantity) pose less task demands on the ability to quantify discrete objects in great apes (Hanus & Call, 2007) or amounts of non-solid substances in human infants (Gao, Levine, & Huttenlocher, 2000; VanMarle & Wynn, submitted for publication). To model tasks of varying complexity, we presented each task differing either by a ratio 1:2 or a ratio 1:4. If performance breaks down irrespective of task complexity, then most likely a full breakdown of object representation occurred. However, if apes perform better in less complex conditions then most likely the representation was impaired but not destroyed.

2. Experiment 1

With the first experiment, we attempted to confirm that non-human primates, in contrast to 10- to 12-months-old infants, succeed in representing and quantifying solid objects that are split into two identical halves. It is possible that brown lemurs' relative success with split objects was related to the methodology used (Mahajan et al., 2009). Perception-based measures may reveal more subtle intuitions than the action paradigm implemented to test human infants. Thus, we adopted the forced choice task of Cheries and colleagues (2008) to assess apes' ability to represent and quantify split crackers in situations of varying complexity (i.e., presenting quantities differing either by a ratio 1:2 or a ratio 1:4). If apes fail to quantify in response to fission events, their performance in conditions of varying complexity may shed light on the reason for their failure. If the apes' object representations are fully destroyed, we expect performance breakdown for both proportions. However, if fission merely overwhelms apes' representational resources (thus limiting their function to support comparative judgements) apes might still succeed for the less difficult 1:4 proportions.

2.1. Method

2.1.1. Participants

Eight great apes (three gorillas [*Gorilla gorilla*] and five orangutans [*Pongo pygmaeus*]) participated in Experiment 1. All apes were housed at the Wolfgang Köhler Research Center (Leipzig zoo) in Germany. All had prior experience with various experiments investigating physical and social cognition. Apes were tested alone either in an indoor observation room or in their sleeping room, respectively. Mothers with children younger than 3 years of age were tested in company of their offspring.

2.1.2. Materials

The stimuli were pieces of wheat crispbread. They measured 6 cm × 5.5 cm (*big* cracker, see Fig. 2 "initial presentation"), 3 cm × 5.5 cm, or 3 cm × 2.7 cm, respectively (*small* crackers, see Fig. 2 "comparison ratios 1:2 or 1:4"). To ensure that the single big cracker would split into two exactly identical halves, the desired breaking line was pre-carved on the backside of the cracker. This manipulation was not visible to the participants. The crackers were placed into two oblong opaque cups (9 cm diameter, 17 cm high). Once the cracker pieces were placed into the cups, the apes could not see them anymore.

2.1.3. Design and procedure

The ape sat behind a Plexiglas panel. A testing surface (slide table) was fixed by a metal frame directly underneath the panel, and the two cups were placed on top of it (58 cm apart of each other). The Plexiglas panel had two holes through which the ape could point at the cups. The experimenter sat in front of the slide table. The slide table was constructed such that its surface could be shifted back and forth. The experimenter pulled the table back and baited the cups in full view of the ape. Procedure was analogous as described by Cheries et al. (2008, p. 429). The apes were presented with two conditions, a "split-in-halves condition" and a "no-split condition". Each condition consisted of one session with six trials. In the split-in-halves condition, the experimenter held out a single big cracker (see Fig. 2, "initial presentation") and broke it in two identical halves before placing it into a cup. The other cup was baited with a cracker of only half (comparison ratio 1:2) or a quarter (comparison ratio 1:4) of the size the original single big cracker. To prevent biasing the subject by stimulus enhancement, the smaller cracker amount was always handled in a similar manner (i.e., grasping it alternately with both hands) and for an equal amount of time before placing it into the cup. After the baiting, the experimenter pushed the sliding table to the panel. The ape could now point at the cup of his choice. The experimenter drew the table back again and handed over the content of the chosen

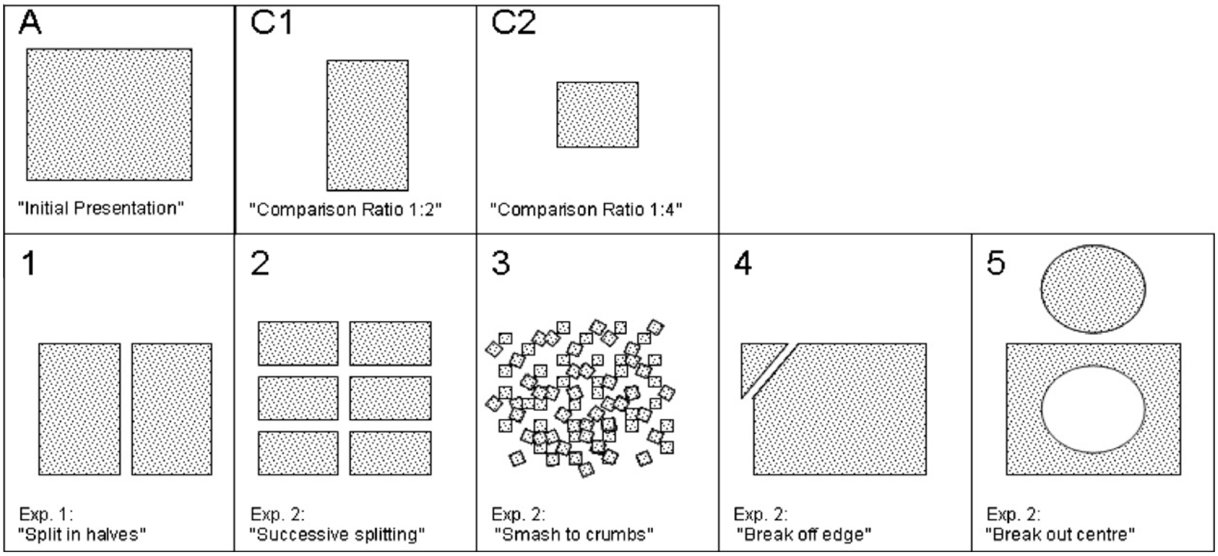

Fig. 2. Schematic depiction of stimuli used in Experiments 1–2.

cup to the ape. The no-split condition was identical to the split-in-halves condition, except that apes never witnessed a splitting but were directly presented with two identical cracker halves. The experimenter did not place the crackers into the cup unless the apes watched her doing so. Condition (split-in-halves condition and no-split condition), cup ratio (1:2 and 1:4), side (larger amount of food in the left or right cup), and order of presentation (larger amount of food placed first or second) were counterbalanced across participants.

2.1.4. Data scoring and analysis

We videotaped all trials and scored them live on coding sheets. We analyzed both first trial and overall performance on the various conditions. We also assessed the occurrence of learning by comparing the performance in the first half and the second half of the trials.

2.2. Results

Fig. 3 presents the percentage of trials in which subjects selected the larger quantity of crackers. Subjects selected the larger of two quantities above chance levels in all conditions (Wilcoxon test: split 1:2: $z = -2.392$; no-split 1:2: $z = -2.041$; split 1:4: $z = -2.251$; no-split 1:4: $z = -2.251$; $p < .05$ in all cases). There were no species differences in any condition except that orangutans selected the larger cracker quantity more often in the split-in-halves condition for a ratio 1:2 (Mann–Whitney test: $z = -2.251$; $p < .05$). Overall, there was no significant difference between the split-in-halves condition and the no-split condition (Wilcoxon test: $z = 0.342$, $p = .73$) or between the two cup ratios (Wilcoxon test: $z = -1.691$, $p = .09$). Similarly, there were no differences between conditions in the first trial (Sign test: 1:2: $p = .69$; 1:4: $p = 1.00$) and no differences between conditions within each ratio (Wilcoxon test: 1:2: $z = -1.841$, $p = .07$; 1:4: $z = -1.300$, $p = .194$).

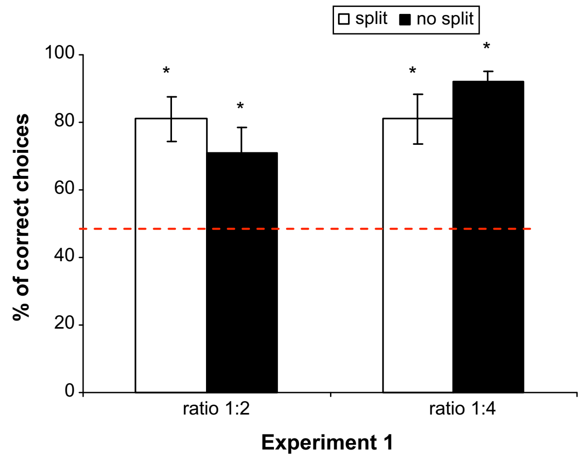

Fig. 3. Percent of correct choices in Experiment 1 ("no-split" and "split-in-halves" conditions), for cup amounts differing by a ratio 1:2 and 1:4. $^{*}p < .05$.

Finally, there was no evidence that subjects improved performance during testing assessed by comparing the first three trials with the second three trials (Wilcoxon test: split 1:2: $z = -1.289$, $p = .20$; no-split 1:2: $z = -0.756$, $p = .45$; split 1:4: $z = -0.137$, $p = .89$; no-split 1:4: $z = -0.447$, $p = .66$).

2.3. Discussion

Apes were able to quantify amounts of solid objects that were split into two halves. That is, their object representations clearly survived fission-type cohesion violations. This confirms the findings of Mahajan et al. (2009) that non-human primates react like 16-months-old infants and human adults when observing splitting events. In contrast to the brown lemurs tested by Mahajan et al. (2009), the apes in the present study were tested with the same forced choice action paradigm as was used in human infants. Thus, the observed difference between great apes and 10- to 12-months-old human infants may not be explained by methodological differences. It seems likely that this difference is developmental in nature (rather than being species-depended). The main developmental change in human infants was observed between 12 and 16 month of age. Because apes were found to develop cognitive capacities in even greater speed than human infants (Gómez, 2005), adult great apes' lesser vulnerability to fission events appears to be a consequence of their advanced cognitive development. Thus, the present findings support the hypothesis that knowledge of cohesion as a cognitive core property arose early in phylogenetic development and is shared with other non-human primate species.

Another goal of the present studies was to investigate whether the probability that apes succeed in quantifying split objects varies as a function of the type of fission presented. In the next experiment, we compared apes' responses to variants of fission events that either increased or decreased an object's non-cohesiveness compared to a split-in-halves.

3. Experiment 2

Apes' ability to represent and quantify objects may vary across variants of fission events which more or less increase an object's non-cohesiveness. In Experiment 2, we compared apes' performance in the context of four events either increasing or decreasing an objects' non-cohesiveness. The questions were first, whether apes' ability to represent would eventually collapse in the context of very strong cohesion violations and second, whether the impact of observed fission would increase as a function of the degree of non-cohesiveness produced by them (i.e., the resulting spatial ambivalence).

Two factors increasing non-cohesiveness are first, the number of resulting elements and second, the temporal structure of the original objects' disassembly. For example, it may be more difficult to maintain a stable object representation if an object is split into multiple small pieces (than only into two as in Experiment 1). Also, object representations may be more affected if the disassembly occurs in one moment than when an object erodes slowly and successively (thereby facilitating the conservation of the initial representation). On the other hand, representations may be less affected by fission events with a low impact on perceived cohesion. For example, fission events that preserve an objects' outer contour have a low impact on an object's boundedness (rigidity of contour) and should thus pose less demands on apes' representational resources.

Apes were presented with four types of fission events either increasing or decreasing an objects' non-cohesiveness compared to a split-in-halves. Events increasing non-cohesiveness were (a) an event in which a cracker was successively broken into six small pieces and (b) an event in which the same cracker was smashed into crumbs in one blow. Thus, in both cases the fission resulted in a higher degree of spatial ambivalence than a split into two halves. Events decreasing non-cohesiveness were (a) an event in which a circle was broken out of the center of the single big cracker and (b) an event in which only a small edge was broken off the original single big cracker. Thus, in both events the cracker was again split into two (now non-identical) halves, however, in contrast to the split-in-halves, the original cracker largely preserved its shape through the fission event. We expect that the successive-splitting and the smashing manipulations will affect apes' performance more than the spilt in halves condition from Experiment 1. In contrast, we expect that the breaking of the edge and breaking out the center will affect apes' performance less than the spilt in halves presented in Experiment 1. Again, we tested if a potential failure occurs independently of task complexity (and thus is most likely connected to a representational breakdown).

3.1. Method

3.1.1. Participants and materials

The same great apes as in Experiment 1 also participated in Experiment 2. Again all materials were made out of pieces of crispbread. In addition to the two opaque cups, one transparent cup was used to present the cracker after the smash manipulation (before filling it into the opaque cup, see below).

3.1.2. Design and procedure

Design and procedure were the same as in Experiment 1, except that instead of splitting the single big cracker into two identical halves, the apes were presented with four new types of splitting manipulations producing varying degrees of non-cohesiveness: the successive-splitting in six parts, the smash in one blow, the breaking off of an edge, the breaking out of the center (see Fig. 2). Recall that the main factors mediating non-cohesiveness are proposed to be (i) the resulting spatial ambiguity (i.e., number of resulting elements), (ii) the temporal structure of the objects' disassembly and (iii) the degree of shape-preservation through fission. On the base of these factors we may approximate how the different splitting events map onto non-cohesiveness and suggest the following ranking. Smashing the cracker in one blow produces the most non-cohesiveness. It results in the highest degree of spatial ambiguity, the disassembly occurs in a very short time frame and the original objects shape is fully abrogated. In fact this manipulation transforms an object into a substance (and thus into a "non-object entity"). The successive-splitting produces the second largest degree of non-cohesiveness, because the resulting spatial ambiguity is high and the shape of the original object is destroyed. However, its slow erosion facilitates the conservation of the object representation. The split into two halves (used in Experiment 1) is in an intermediate position, resulting in a comparatively low spatial ambiguity, but affecting the shape. Finally, the breaking off of an edge and the breaking out of the center result in the lowest degree of non-cohesiveness, because they produce a comparatively low spatial ambiguity and preserve the original objects shape. The four manipulations presented in Experiment 2 are described below.

In the "successive-splitting condition", the experimenter held out a single big cracker (see Fig. 2, "initial presentation") and successively broke it into six small pieces. Each of the pieces was directly placed into the cup after it was broken off the original cracker. Thus, the single big cracker appeared to be gradually melting down. Again the other cup was baited with a cracker of only half (comparison ratio 1:2) or a quarter (comparison ratio 1:4) of the size the original single big cracker. In the "smash-to-crumbs condition", the experimenter held out the single big cracker and then crushed it by closing her hand. Then she opened the hand again and filled the resulting cracker crumbs into a transparent cup. Then she poured the content of the transparent cup in full view of the ape into the opaque cup. The other cup was baited with a cracker of only half (comparison ratio 1:2) or a quarter (comparison ratio 1:4) of the size the original single big cracker. In the "break-out-center condition", a circle was broken out of the center of the single big cracker. Thus, the cracker was again split into two halves, but the outer contour remained unchanged. Again the other cup was baited with a cracker of only half (comparison ratio 1:2) or a quarter (comparison ratio 1:4) of the size the original single big cracker. In the "break-off-edge condition", only a small edge was broken off the original single big cracker. Again, in contrast to the split-in-halves condition of Experiment 1, the original cracker largely preserved its shape through the fission event. The other cup was again baited with a cracker of only half (comparison ratio 1:2) or a quarter (comparison ratio 1:4) of the size of the original single big cracker. To prevent any biases created by stimulus enhancement, the smaller cracker amount was handled in a similar manner (i.e., grasping it alternately with both hands) and for an equal amount of time before placing it into the cup.

All apes received two blocks (ratio 1:2 and ratio 1:4) with four conditions. All apes first received a block with a ratio 1:4 followed by a block with a ratio 1:2. Over both blocks, the conditions were administered in a quasi-randomized fashion (e.g., block 1: edge–center–succession–smash; block 2: smash–succession–center–edge). Each condition consisted of six trials. Again side (larger amount of food in the left or right cup) and order of presentation (larger amount of food placed first or second) were counterbalanced across participants.

3.1.3. Analysis

We carried out the same analyses as in Experiment 1. In addition, we compared the overall performance in the four test conditions of Experiment 2 with the split-in-halves condition of Experiment 1 (which was solved equally well as in the no-split condition and may thus serve as a baseline). Further, we compared the overall performance for the two cup ratios in Experiments 1 and 2.

3.2. Results

Fig. 4 presents the percentage of trials in which subjects selected the larger quantity of crackers. Subjects failed to

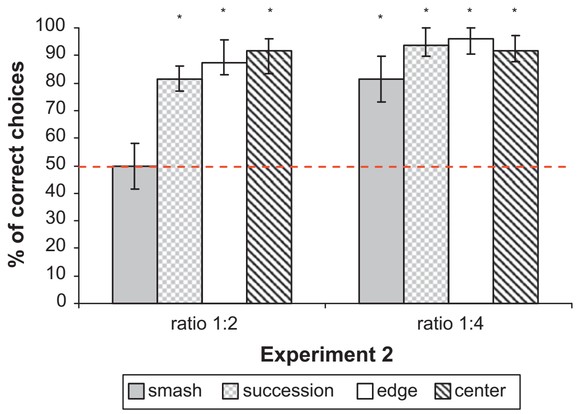

Fig. 4. Percent of correct choices in Experiment 2 ("successive-splitting", "smash-to-crumbs", "break-off-edge" and "break-out-center" conditions) for cup amounts differing by a ratio 1:2 and 1:4. $^{*}p < .05$.

select the larger of two quantities in the smash-to-crumbs condition when cups differed by a ratio 1:2 (Wilcoxon test: $z = -.138$, $p = .890$). In all other conditions, they performed above chance level (Wilcoxon test: smash 1:4: $z = -2.264$, $p < .05$; succession 1:2: $z = -2.549$, $p < .05$; succession 1:4: $z = -2.646$, $p < .01$; edge 1:2: $z = -2.449$, $p < .05$; edge 1:4: $z = -2.714$, $p < .01$; center 1:2: $z = -2.588$, $p < .05$; center 1:4: $z = -2.640$; $p < .01$). There were no species differences in any of the conditions tested.

Overall, apes' performance across conditions reliably differed (Friedman test: $\chi 2 = 10.57$, $df = 3$, $p < .05$, $N = 8$). Apes performed reliably better in the "successive-splitting condition, the break-out-center condition, and the break-off-edge condition than in the smash-to-crumbs condition (Wilcoxon test: succession: $z = -2.386$; edge: $z = -2.252$; center: $z = -2.392$, $p < .05$ in all cases). However, their performance between the break-out-center condition, the break-off-edge condition, and the successive-splitting condition did not differ (Wilcoxon test: edge/succession: $z = -1.414$, $p = .16$; center/succession: $z = -1.265$, $p < .21$; edge/center: $z = -0.000$, $p = 1.00$) Further, the apes overall reliably more often selected the larger amount for a ratio 1:4 than for the ration 1:2 (Wilcoxon test: $z = -2.375$, $p < .05$).

Also within a ratio 1:2, apes' performance differed between conditions (Friedman test: $\chi 2 = 10.52$, $df = 3$, $p < .05$, $N = 8$). This difference was not apparent for a ratio 1:4 (Friedman test: $\chi 2 = 6.75$, $df = 3$, $p = .08$, $N = 8$). Further, there were no differences between conditions in the first trial (Sign test: $p = .13$ in all cases).

Finally, there was no evidence that subjects improved performance during testing assessed by comparing the first three trials with the second three trials (Wilcoxon test: succession 1:2: $z = -1.633$, $p = .11$; succession 1:4: $z = -1.000$, $p = .32$; smash 1:2: $z = 0.000$, $p = 1.00$; smash 1:4: $z = -1.633$, $p = .11$; edge 1:2: $z = -1.414$, $p = .16$; edge 1:4: $z = -0.000$, $p = 1.00$; center 1:2: $z = -0.000$, $p = 1.00$; center 1:4: $z = -1.000$, $p = .32$).

3.2.1. Overall impact of event and ratio in Experiments 1–2

Overall, apes' performance in events with increased non-cohesiveness did not reliably differ from the split-in-halves condition of Experiment 1 (Wilcoxon test: smash: $z = -1.367$, $p = .17$; succession: $z = -1.472$, $p < .14$). However, apes performed reliably better in both events with decreased non-cohesiveness than in the split-in-halves condition of Experiment 1 (Wilcoxon test: edge: $z = -2.226$, $p < .05$; center: $z = -2.226$, $p < .05$). Also, the apes more often selected the cup containing the greater cracker amount for a ratio 1:4 than for the ration 1:2 (Wilcoxon test: 1:2: $z = -2.527$, $p < .05$).

3.3. Discussion

Apes generally performed well in all test events. Even though their performance reliably differed across conditions, they performed above chance in all events except the one producing the highest degree of non-cohesiveness. Apes failed to quantify amounts of a cracker that was smashed into crumbs before filling it into the cup. This effect was observed only for cup amounts differing by a ratio 1:2. This suggests that apes ability to represent and quantify may indeed be impaired by fission. In contrast to a split-in-halves, the smash represented a very strong instance of cohesion violation. The original cracker piece was heavily fragmented, and fragmentation occurred in a very short time period, both factors handicap the conservation of object representation through fission. However, even in the face of this strong interference, apes' representations were not fully destroyed, since apes succeeded with a ratio 1:4. Note that such success weakens the explanation based on simply disliking smashed crackers. Otherwise they should have also failed to choose the smashed (yet larger) cracker in the ratio 1:4. Moreover, note that even in the ratio 1:2 they did not systematically avoid the smashed cracker, they were merely indifferent.

In all other conditions, apes performed reliably above chance. In contrast to the smash, the successive-splitting did not impede apes' quantity judgements. Contrary to our expectation apes performed even slightly better than after witnessing a split into two halves. Even though the cracker was divided in many more pieces than by a split into two halves, the apes still succeeded to represent and quantify cracker amounts. It seems very likely that the apes profited from the long and slow erosion of the original cracker facilitating the survival of object representations. As suggested in the introduction, in this case it might be easier to track the original object through fission events. Thus, the smash manipulation increased the non-cohesiveness of the cracker much more than the successive-splitting. First, the smash results in a much greater number of very small fragments, rendering the resulting mass "substance-like". Second, the duration of the fragmentation process is much shorter for smashed crackers. Apparently, together they produce too great costs, and the apes fail to correctly assess the quantities involved.

Further, apes also successfully quantified crackers in events with decreased non-cohesiveness, showing high rates of correct choices for both types of fission events with a low impact on an object's boundedness. Breaking out the center and breaking off an edge had reliably less impact than fully smashing the cracker and also less impact than the split into two identical halves presented in Experiment 1. This suggests that fission events with a low impact on an objects' contour (and thus, a lower impact on an objects' boundedness) also pose lesser demands on apes' representational resources. However, both conditions (center/edge) did not differ from events where the cracker eroded only slowly over time (succession).

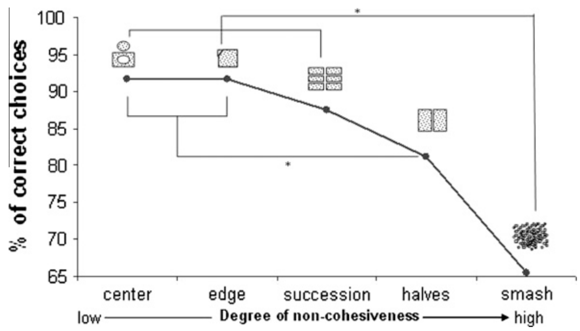

Fig. 5. Percent of correct choices as a function of the non-cohesiveness/spatial ambiguity resulting from the fission events used in Experiments 1–2. *$p < .05$.

Together, these results suggest that the impact of various fission events is a function of produced non-cohesiveness which appears to be mediated mainly by the factors spatial ambiguity and shape-preservation (see Fig. 5).

Apes' performance was lowest in the smash condition which produced the highest degree of spatial ambiguity and had the greatest impact on the objects' original shape. Apes' performance was highest in the center and edge conditions which produced a comparatively low degree of spatial ambiguity and had the lowest impact on the objects' shape. Further, apes performed well in the succession condition even though the cracker was substantially fragmented. This appears to be connected to the slow and successive fragmentation keeping spatial ambiguity comparatively low. Note that this interpretation is at least partially complicated by the fact that apes were presented with the split in half in Experiment 1 before they were tested with all other variants of fission in Experiment 2. It can thus not be completely ruled out that also order effects co-determined apes' behavior across conditions. However, given that apes did not learn in any of the conditions and performed lowest in the smash condition of Experiment 2, it seems unlikely that order effects had a substantial impact on apes' behavior in these tasks.

Finally, apart from the type of fission event also the proportionate ratio between cup contents influenced the behavior of apes in this series of experiments. This confirms the previous finding that quantity judgements involving higher ratios are more difficult to solve for great apes (Hanus & Call, 2007).

4. General discussion

Great apes were able to quantify split solid objects in the context of various fission events. They were able to quantify crackers split into two identical halves or crackers eroding slowly over time. They showed even higher rates of success if only a small edge was broken off or the center was broken out of the original cracker. Thus overall, apes' object representations appear to be highly robust in the context of fission events. However, they were not immune to disruption because their quantifications broke down if the cracker was fully fragmented.

As brown lemurs and 16-months-old human children, but in contrast to 12-months-old human infants, apes managed to represent and quantify a solid cracker that was split into two halves. In contrast to the lemurs tested by Mahajan et al. (2009), the apes in the present studies were tested with a similar action task as was used in the infant studies. Thus, our results confirm the existence of a developmental trend in the perception of fission-type cohesion violations (with non-human primates appear to behave more like 16-months-old children and adults). In addition, the present studies revealed that apes also validly judge quantities in a variety of other fission events. For example, apes were even more likely to correctly assess quantities in fission events with a low impact on an objects' boundedness (i.e., fission events with low impact on the outer contour). Thus, the two constitutes of perceived cohesion are not equally important to carry forward the impression of a persisting object, but at least in some instances, boundedness may outweigh connectedness. Also apes were able to correctly quantify amounts of objects that eroded only slowly over time.

Only in the case of a very strong cohesion violation (i.e., when the cracker was fully fragmented), the apes' quantity judgements eventually collapsed. What brought about this performance breakdown? First of all, by fully fragmenting the cracker we rendered it "substance-like". Note, that events involving a solid object (that is, an entity for which an object representation is already established) being transformed into a substance cannot be compared with events involving a substance (a non-object entity) from the outset. We can thus not simply attribute apes' performance breakdown to a general failure to address substances as continuously existing entities as it was observed in infants (Huntley-Fenner et al., 2002). A second possibility is that pouring the smashed cracker-substance from one location to the other confused the object-tracking mechanisms. However, this assumption is challenged by the fact that in many instances the apes perfectly traced and quantified the smashed cracker-substance. A more likely hypothesis is thus that the fission manipulation disrupted apes' object representations. However, in no case, apes' representations fully broke down. They never appeared to lose object permanence after experiencing cohesion violations. To the contrary, if the task demands were reduced (i.e., tasks involving a larger proportionate difference), apes did well in all cases and even managed to quantify fully fragmented pieces of cracker. Thus, the present results strongly suggest that even strong incidences of fission did not fully destroy apes' object representations but limited their operational capability as was observed in adults (Mitroff et al., 2004). Note that also the findings of Cheries et al. (2008) might be interpreted along this line: If infants actually had failed to experience the split object as permanent they should have shown an above-chance preference for the cup containing the intact (small) cracker which was not the case. A potential caveat of the present study is that it does not allow deciding which of the factors present in the smash manipulation eventually provoked the breakdown. The fission in the smash condition occurred quickly and resulted in many small pieces. Further research is needed to disentangle the respective impact of these two dimensions that are left confounded.

Overall, these findings suggest that fission events vary in their impact on representational abilities. The more a specific fission event increases an object's non-cohesiveness the greater its impact on object representations. As suggested by Chiang and Wynn (2000), the problems created by increasing non-cohesiveness may be connected to the resulting spatial ambiguity which produces high cost for tracking abilities. Also the findings of vanMarle and Scholl (2003) emphasize spatial ambiguity as a main factor complicating adults' object tracking. For example, adults experienced less difficulty in tracking a non-cohesive collection that moved as a fixed local image cluster than a non-rigid substance expanding and contracting. In addition, our findings suggest that also shape invariance (stability of contour) has a major impact on apes' perception of cohesiveness.

Finally, the present findings offer important insights into the nature of apes' representations supporting the quantity judgements in these tasks. Current literature discusses two prominent classes of models characterizing the format of quantity representations (Feigenson et al., 2002). One class of models suggests that quantities are represented as a single analogue magnitude (Gallistel & Gelman, 1992; Whalen, Gallistel, & Gelman, 1999; Wynn, 1998). In this case, the discriminability of quantities would be a function of their ratio (as suggested by Weber's Law). The mental magnitude can serve both as a representation of discrete quantities (being proportional to number) or as a representation of continuous quantities (being proportional to the total surface or volume). Our results suggest a major impact of ratio on apes' quantity judgment. However, even though ratio-dependence is the main signature property of all analogue magnitude models they cannot fully explain apes' behavior in the present studies. Relying solely on analogue magnitudes, apes would not have been able to discriminate between different test conditions because the amounts presented were exactly the same. Even more, fission should in no case have affected their judgements, because the amounts remain unchanged by fission. A second class of models proposes that quantities are represented as distinct symbols in an "object-file" format containing primarily spatiotemporal information (Kahneman & Treisman, 1984; Kahnemann, Treisman, & Gibbs, 1992; Leslie et al., 1998; Pylyshyn, 2001; Uller, Carey, Huntley-Fenner, & Klatt, 1999). In this case, each object in an array is represented by a symbol (an object-file) for that distinct object, regardless of its features/properties, the main signature property of this type of mechanisms being its fixed capacity limit (i.e., 3–4 objects). The object-file model better agrees with our finding that fission may affect quantity judgments. The more a fission event increases an objects' non-cohesiveness the greater the resulting spatial ambiguity and the greater apes' difficulties to track the remaining parts of the object. The full fragmentation of an object fully disrupted the objects' spatiotemporal path, produced the highest degree of spatial ambiguity, and thus, interrupted the one-to-one-correspondence between the object-file and the object itself. However, also the object-file account is not fully commensurable with our findings. First, apes' quantifications were markedly ratio-dependent (i.e., they reliably more often chose the cup containing the greater amount in task involving a larger proportionate difference). Second, apes also succeeded with amounts higher than expected by the capacity limit. Thus, the present study does not allow us to decide between these two models, but strongly suggests that aspects of both types of processing were involved in apes' quantity estimations.

In sum, cohesion as a foundational principle to perceive and reason about persisting objects appears to have a long evolutionary history and is shared also by our closest non-human primate relatives, the great apes. As a consequence, also great apes appear to be influenced by the perception of cohesion violations. The fission-type violations presented here affected apes' representational abilities, however, they did not destroy their representations of persisting objects. Instead, the impact of fission on object representations appears to be a function of their power to increase non-cohesiveness. At least in humans, the vulnerability to fission events seems to decrease during the ontogenetic development. At present, we do not now if such ontogenetic shift also occurs in non-human primates. The present studies cannot shed light on these early developmental processes, because the great majority of apes tested here were adults. Future research may explore in more detail how the cohesion principle operates on object representations over both ontogenetic and phylogenetic development.

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