The source of visual size adaptation

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Size adaptation describes the tendency of the visual system to adjust neural responsiveness of size representations after prolonged exposure to particular stimulations. A larger (or smaller) adaptor stimulus influences the perceived size of a similar test stimulus shown subsequently. Size adaptation may emerge on various processing levels. Functional representations of the adaptor to which the upcoming stimulus is adapted may be coded early in the visual system mainly reflecting retinal size. Alternatively, size adaptation may involve higher order processes that take into account additional information such as an object's estimated distance from the observer, hence reflecting perceived size. The present study investigated whether size adaptation is based on the retinal or the perceived size of an adaptor stimulus. A stimulus' physical and perceived sizes were orthogonally varied using perceived depth via binocular disparity, employing polarized 3D glasses. Four different adaptors were used, which varied in physical size, perceived size, or both. Two pairs of adaptors which were identical in physical size did not cause significantly different adaptation effects although they elicited different perceived sizes which were sufficiently large to produce differential aftereffects when induced by stimuli that physically differed in size. In contrast, there was a significant aftereffect when adaptors differed in physical size but were matched in perceived size. Size adaptation was thus unaffected by perceived size and binocular disparity. Our data suggest that size adaptation emerges from neural stages where information from both eyes is still coded in separate channels without binocular interactions, such as the lateral geniculate nucleus.

Introduction

Adaptation is a general principle of sensory processing, which describes the tendency of sensory systems to adjust neural responsiveness after prolonged exposure to particular stimulations. It has been reported across different sensory systems, such as vision (Kohn, 2007), audition (Dix, Hallpike, & Hood, 1949; Westerman & Smith, 1984), olfaction (Dalton, 2000), and vibro-tactile sensation (Cohen & Lindley, 1938; O'Mara, Rowe, & Tarvin, 1988), and has been ascribed different functional roles. While facilitative effects were found for the discrimination of faces after adaptation (Oruç & Barton, 2011), or for amplitude discrimination after vibrotactile adaptation (Goble & Hollins, 1993), other studies showed that adaptation could also impair discrimination ability, such as in the case of vibrotactile adaptation, which has been shown to affect fine discrimination (Hollins, Washburn, & Bensmaïa, 2001). Importantly, adaptation has been

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proven in the above studies to be a versatile tool to compare and relate the neural representations of sensory and cognitive processes. In particular, the way adaptation transfers from one experimental condition to another allows determining whether both conditions involve identical neuronal populations or whether they rely on distinct neural representations.

One particularly interesting example of visual adaptation is the size adaptation illusion during which a prolonged presentation of a stimulus alters the perceived size of a subsequently shown test stimulus with a similar shape shown at the same location (Blakemore & Sutton, 1969; Pooresmaeili, Arrighi, Biagi, & Morrone, 2013; Kreutzer, Fink, & Weidner, 2015). If the adaptor is larger (or smaller) than the test stimulus, the perceived size of the subsequently presented test stimulus is decreased (or increased, respectively). The perceptual changes triggered by size adaptation are accompanied by changes in neural activity in human primary visual cortex, V1 (Pooresmaeili et al., 2013). This finding is in line with a number of functional imaging studies demonstrating that subjective perceived size, e.g., as modulated by illusionary context, alters the retinotopic representation in V1 (Fang, Boyaci, Kersten, & Murray, 2008; Murray, Boyaci, & Kersten, 2006; Schwarzkopf, Song, & Rees, 2011; Sperandio, Chouinard, & Goodale, 2012). These studies suggest that a feedforward, i.e., bottom-up retinal size signal is transformed by continuously integrating context information. More specifically, the retinal size signal is altered by feedback possibly from extrastriate regions, hence generating a neural code that represents perceived size.

In line with these findings, Pooresmaeili et al. (2013) put forward a model suggesting that size adaptation is generated in V1. The model assumes that the contours defining the adaptor induce inhibitory local aftereffects in V1. These aftereffects are thought to alter the spatial distribution of contour representations of a subsequently presented (test) stimulus, hence changing its perceived size. This account has implications with regard to the predicted behavioural features of size-adaptation. In particular, if V1 is indeed the origin of size adaptation and at the same time codes apparent size, then both effects should be interrelated. Consequently, the postulated inhibitory local aftereffects should be driven by V1 representations, which are known to represent perceived size. Thus, size adaptation is expected to be based on, or should at least be modulated by, changes in perceived size.

Alternatively, the relevant mechanisms underlying size adaptation may occur prior to V1 on processing levels that contain unaltered retinal size representations. The effects previously observed in V1 would then reflect the consequences rather than the generative mechanisms of size adaptation. Size adaptation would then be expected to be driven by retinal size independent of any changes in perceived angular size. The candidate region that may account for subcortical size adaptation is the lateral geniculate body (LGN), which has previously been demonstrated to show adaptation to high contrast stimuli reducing contrast sensitivity within its magnocellular layers (Solomon, Peirce, Dhruv, & Lennie, 2004).

Hence, in order to investigate whether size adaptation is altered by changes of the perceived angular size, it is mandatory to separate these effects from those induced by retinal size changes. Thus, in the present experiment, perceived and retinal sizes were varied orthogonally by changing an adaptor's binocular disparity using polarized 3D goggles. Binocular disparity defines the positional difference between the two retinal projections of a given point in space (Qian, 1997). The brain can determine this positional difference by matching corresponding representations from both retinas and can thus use it to extract depth information. Hence, experimental variations of disparity alter an adaptor's apparent distance and consequently, via size distance scaling, its perceived size. This procedure allows creation of (a) adaptor stimuli of identical retinal size, which are perceived differently, and (b) adaptors of different retinal sizes, which are perceived the same. This dissociation between an adaptor's perceived size and its retinal size permits inferring the neural level underlying size adaptation.

For instance, if size adaptation originates at a level where information from both eyes is already integrated, then size adaptation can be assumed to be sensitive to changes of binocular disparity and, along with it, to perceived size. Specifically, adaptors that are shown at the same retinal size but are perceived differently (i.e., Figure 1A and 1B, the first and third adaptors) should generate distinct adaptation effects (Figure 1B, dotted line). In that case, size adaptation most likely originates in cortical regions, since neurons coding binocular disparity are found in primary visual cortex and higher visual regions (Cumming & DeAngelis, 2001; Neri, Holly, & Heeger, 2004). On the other hand, if size adaptation is generated earlier in the visual system where information from both eyes is still coded in separate channels such as in the lateral geniculate body of the thalamus (LGN), then size adaption is expected to depend on retinal size representations. Particularly, adaptors with different physical sizes but equivalent perceived size (i.e., Figure 1A and 1B, the first and fourth adaptors) would be expected to generate different adaptation effects (Figure 1B, solid line). A physically larger adaptor will cause more adaptation than a smaller adaptor, despite both being matched with regard to perceived size.

Additionally, a control experiment assessing individual depth perception for every participant was

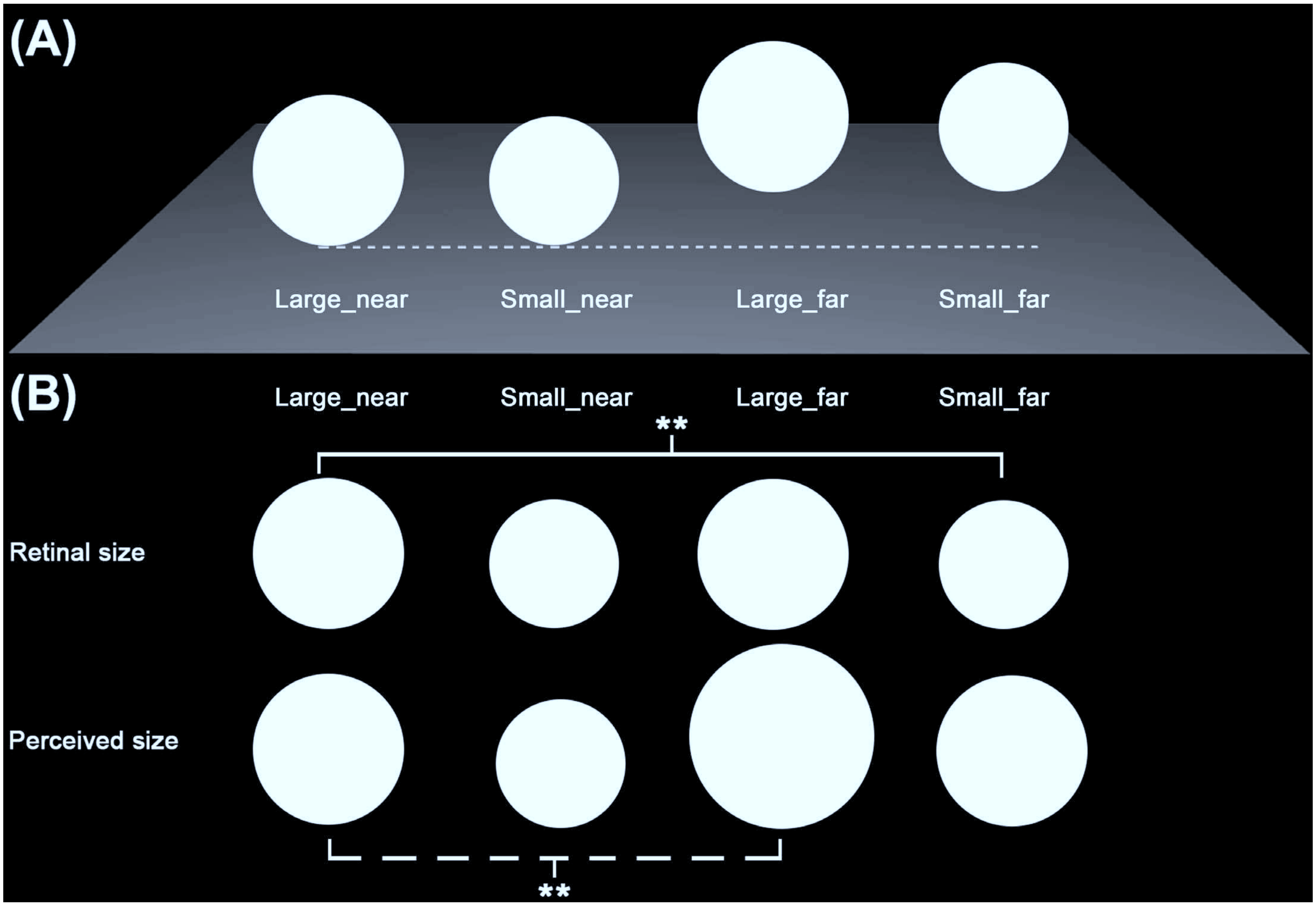

Figure 1. (A) Example of adaptors in four conditions. The Large_near adaptor (2.9° of visual angle) was located at zero depth. The Small_near adaptor was shown at a smaller physical size (2.7° of visual angle) and also at zero depth. The Large_far adaptor (2.9° of visual angle) was shown at individual disparity to introduce an impression of depth. Finally, the Small_far adaptor (2.7° of visual angle) was presented at the same individual disparity as Large_far. Please note that the gray plane in this illustration is used only in order to exemplify depth and was not actually shown during the actual experiment where the impression of depth was created by binocular disparity. Likewise, the gray dash line serves as an auxiliary line to indicate the depth plane of the screen and was also not shown during the actual experiment. (B) Binocular disparity allowed generating specific combinations of retinal and perceived sizes across the different experimental conditions. The retinal size (upper row) and the perceived size (lower row) representations of four different conditions are illustrated separately, as are the predicted effects of size adaptation based on these representations. If size adaptation exclusively depends on retinal size representations (upper row), then size adaptation is expected to be stronger in the Large_near compared to the Small_far condition (indicated by the solid line). Please note that these two conditions are matched with regard to perceived size. Alternatively, if size adaptation is largely based on perceived size (lower row), then the adaptor in the Large_far condition is expected to produce stronger size adaptation than in the Large_near condition, despite the fact that these two conditions are matched with regard to retinal size.

performed in order to verify that binocular disparity indeed generated robust depth perception for participants. Moreover, we carried out another control experiment where changes of perceived size were explicitly measured to ensure that participants indeed experienced the far adaptor as perceptually larger than the near adaptor. We further verified that such a perceptual difference was sufficiently large to produce differential aftereffects when induced by stimuli that physically differed in size.

Experiment 1

Methods

Participants

Twenty participants were enrolled in the current experiment. However, one participant was unable to perceive a 3D effect as induced by disparity and had to be excluded from the study, leaving a final sample of nineteen participants (12 female, seven male; mean age 27.3 years old; age range, 18 to 36 years). None of the participants reported a history of neurological or psychiatric disorders. All participants included had normal or corrected-to-normal vision. Participants were right-handed as measured using the Edinburgh Handedness Inventory (Oldfield, 1971). Written informed consent was obtained prior to the experiment in accordance with the Declaration of Helsinki. Participants were remunerated for their time. The study was approved by the ethics committee of the German Society of Psychology.

Stimuli and procedure

Stimuli were presented on an LG 27MT93s 27-in (581 mm × 363 mm) 3D monitor at a distance of 66 cm. The resolution of the screen was 1920 × 1080 with a refresh rate of 60 Hz. The luminance of the black-and-white display was 0.33 cd/m^2 (background) and 103.40 cd/m^2 (adaptor), respectively. Distance was preserved by a chin and forehead rest. Goggles with polarized lenses were used to perceive the 3D effect of the stimuli. Disparate images were presented to both eyes by rendering them to pixels emitting light with specific polarization. The screen used in the present experiment involved two different types of pixels, which were arranged line-by-line with consecutive lines entailing different light polarizations. This allowed for generating and presenting two disparate images and hence to alter binocular disparity with pixel precision. Stimuli consisted of white circles of 2.7° or 2.9° of visual angle. Throughout the experiment, stimuli were presented on a black background with a white fixation cross positioned at the center.

The experiment comprised three parts, a size matching task, a disparity matching task, and a size adaptation experiment. Participants performed the tasks sequentially in that order. During the size matching task, stimuli were presented in 2D. During the disparity matching task and the size adaptation experiment, stimuli were presented in 3D and participants wore 3D goggles.

The size matching task was conducted to determine any lateralization bias, i.e., to assess if objects are perceived larger when presented on one or the other side of the screen. Second, the disparity matching task determined the individual degree of disparity required to achieve adaptors with equal perceived sizes despite different retinal sizes (2.7° and 2.9° of visual angle). Finally, the size adaptation experiment was performed to compare the amount of size adaptation for four different adaptors (Table 1 and Figure 1).

Adaptors	Disparity (0, Z)	Physical size	Perceived size
Experiment 1			
Large_near	0	2.9° of visual angle	Size X*
Small_near	0	2.7° of visual angle	Size $X-$*
Large_far	Z*	2.9° of visual angle	Size $X+$*
Small_far	Z*	2.7° of visual angle	Size X*
Experiment 2b			
Large_far matched	0	Individually varied	Size $X+$*

Table 1. Disparity, physical size and perceived size of adaptor conditions in Experiment 1 and Experiment 2b. **Note*: The perceived sizes X, $X+$, $X-$ and disparity Z represent individual values as derived from a subjective estimation procedure that preceded the actual experiment.

Matching tasks: Size matching task: In every block of the size matching task, the left circle (2.7° of visual angle) was the test circle and appeared at zero disparity (no impression of depth). Its size was kept constant throughout the experiment. The initial size of the right circle (also zero disparity, no impression of depth), i.e., the probe, was randomized and ranged between 2.5°, 2.6°, 2.8°, and 2.9° of visual angle. Subjects' task was to indicate via button press which of the two circles appeared larger. They were instructed to respond with the index or ring finger of their right hand whether the left or the right circle appeared larger. The size of the right circle, i.e., the probe, changed according to the participants' responses using an adaptive algorithm called Parametric Estimation by Sequential Testing (PEST, Macmillan & Creelman, 1991). This algorithm is designed to find the point of subjective equality (PSE), that is, the point at which no relevant differences between responses to a variable stimulus (here, the probe circle) and a standard stimulus (here, the test circle) can be detected. The PEST algorithm determines the PSE by sequentially varying the size of the probe. If the participant consistently judges the probe to be larger than the test, its size is changed at large steps to make the probe smaller and more similar to the test. Steps become smaller as the participants responses approach chance level. Once the step is as small as a predetermined value (one pixel on the screen), that is, once the size of the probe circle is assumed to reflect the apparent size of the test circle, the PEST algorithm finished the adaptive procedure. Then the experiment moved on to the next block.

Disparity matching task: As in the size matching task, subjects were instructed to indicate with the index or ring finger of their right hand whether the left or the right circle appeared larger. The disparity of the left circle changed according to the participant's responses using the same adaptive algorithm as in the size matching task. Unlike in the size matching task where stimulus size was changed, the PEST algorithm determines the PSE by sequentially varying disparity values in response to the participants' answers in the disparity matching task. For instance, when the subject perceived the right circle as larger, the subject indicated this via a right button press. As a consequence, the disparity of the left circle (i.e., the probe) increased with a certain value determined by the algorithm and with increasing disparity, the stimulus' perceived size increased accordingly. Given the concept of size constancy, the impression of depth was expected to alter perceived size (Fisher, 1968; Gilinsky, 1951). The further away an object is the larger we perceive it as compared to an object of identical retinal size at a very near distance. Thus, increasing disparity and thereby increasing perceived distance enabled us to find the point where the probe (i.e., the smaller circle on the left) in the distance appears to be of the same size as the test circle (i.e., the larger circle on the right) presented nearby, i.e., at zero disparity.

For both size and disparity matching tasks, each trial started with a 500 ms presentation of two circles, located to the left and to the right side of the central fixation cross (2.7° of visual angle distance between the center of the circles and the fixation point). The fixation cross remained at the center of the screen throughout the experiment. The two circles were followed by 2000 ms during which responses were recorded (Figure 2A). Both size and disparity matching tasks consisted of four blocks each. One block consisted of a minimum of five trials and a maximum of twenty trials. The exact number of trials varied based on the PEST algorithm and was determined by the speed at which the adaptive algorithm succeeded and stopped (size matching task: mean number of trials, 6.51; *SD*, 1.63; disparity matching task, mean number of trials, 7.08; *SD*, 1.45). The blocks were separated by breaks, and participants started the next block by pressing a third button.

Size adaptation experiment: Four different adaptors were used and each of them was shown during four blocks with a total of sixteen blocks completely randomized (Table 1 and Figure 1). The first adaptor had a physical size of 2.9° of visual angle and was presented at zero disparity (Large_near), which induces a perceived size of *X*. This adaptor served as a standard stimulus that allowed comparing size adaptation effects of the other three conditions.

In addition, two additional adaptors were used to investigate whether a difference in perceived size or a difference in physical size would have stronger effects on size adaptation. Accordingly, one of the two types of size information was altered while the other was kept constant across different conditions.

First, in order to investigate the effects of retinal size on size adaptation, an adaptor with smaller retinal but similar perceived size was used to initiate size adaptation (i.e., perceived size *X* as the Large_near condition). This retinally smaller adaptor (2.7° of visual angle) was shown further away (Small_far) with a binocular disparity that was carefully derived from the disparity matching task described before. Consequently, perceived sizes of the Small_far adaptor and the Large_near adaptor were identical despite different retinal sizes.

Secondly, to investigate the effects of perceived size on size adaptation, an adaptor with similar retinal but larger perceived size was used to induce size adaptation (i.e., perceived size *X*+), the large adaptor was presented at an individual disparity (i.e., disparity *Z*, the same as Small_far adaptor) to induce an impression of depth. This caused the adaptor to appear further away (Large_far) and was hence perceived as larger (i.e., perceived size *X*+). Particularly, the Large_far adaptor was perceived larger than the Large_near adaptor (i.e., perceived size *X*), despite both having identical retinal size.

Finally, pilot experiments using stimuli without any changes in binocular disparity showed that the size changes induced by size adaptation were stronger the larger an adaptor was relative to the target. This was shown by a significant linear relationship between the size of six adaptors (2.69°, 2.91°, 3.12°, 3.30°, 3.51°, and 3.73° of visual angle) and the corresponding adaptation effects, $F(1,5) = 26.38$, $p < 0.005$. In order to verify that this held also true for the current setting, i.e., to verify that a smaller adaptor led to less adaptation, we compared size adaptation for large (2.9° visual angle; Large_near) and small stimuli (2.7° visual angle Small_near) presented at zero disparity, the latter inducing a perceived size of *X*–. Testing the adaptation effect of the Small_near adaptor with Small_far adaptor could confirm the comparison between the effects of the Large_near and Large_far conditions.

As in the matching tasks, estimation of perceived size and hence measuring the strength of size adaptation was assessed using the PEST algorithm. The number of trials depended on the convergence of the PEST algorithm and varied between five and twenty trials (mean number of trials: 8; *SD*: 2.80). There were rest breaks between blocks. Participants were able to control their resting times and started the next block by pressing a third button.

Trials during the size adaptation experiment differed from the matching tasks insofar that the test and the probe were preceded by one adaptor shown on the left side at the same position at which the test circle appeared subsequently. Each trial started with the adaptation display, which lasted 5000 ms, and was followed by a 500 ms interstimulus interval, during which only the fixation cross was present (Figure 2B). The adaptor circle flickered at 4 Hz to prevent any formation of an afterimage that could interfere with the illusions (Sperandio, Lak, & Goodale, 2012). The display of the test stimuli lasted for 200 ms and always contained two circles (test and probe) as for the size

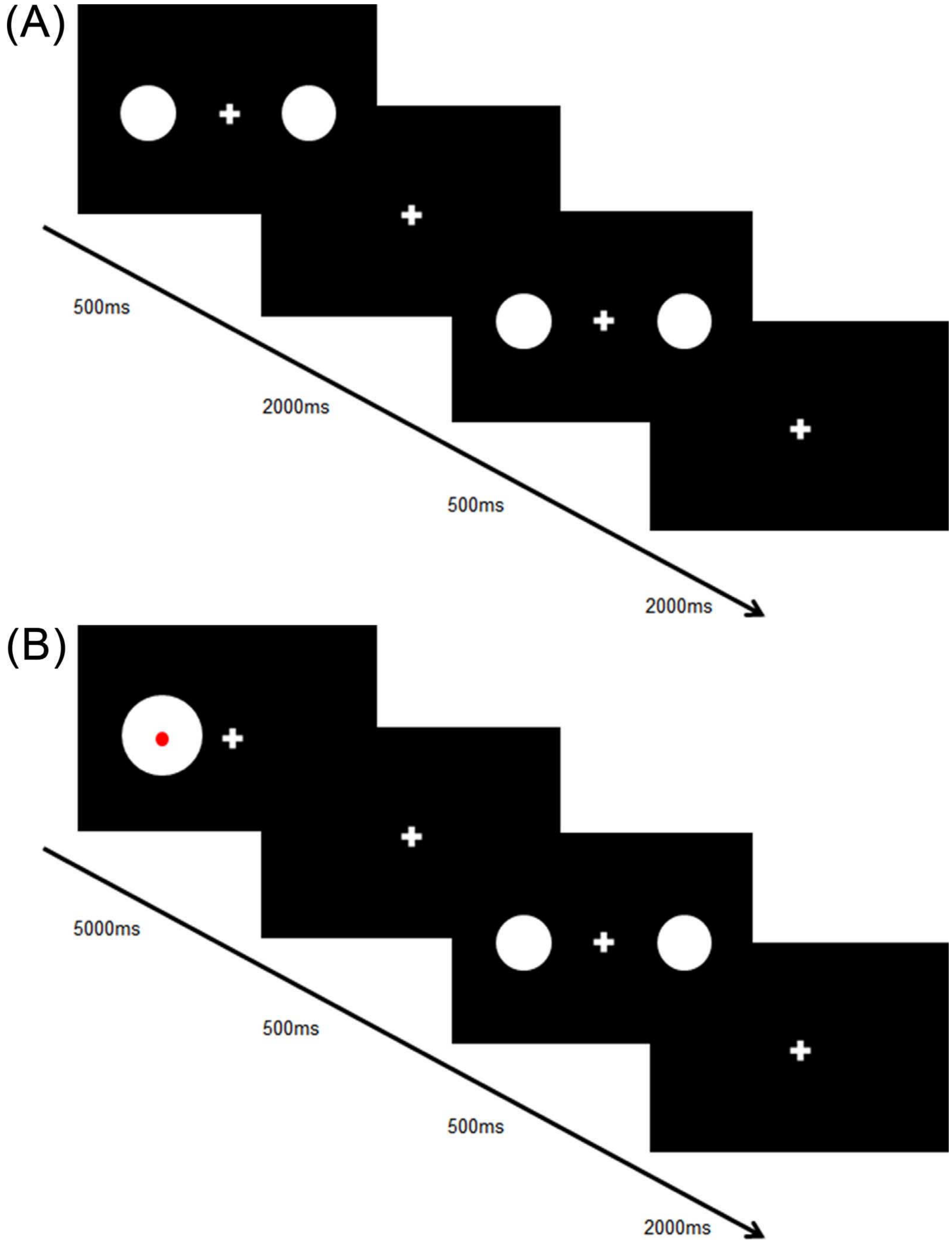

Figure 2. (A) Procedure of the size and disparity matching tasks: Each trial started with a 500 ms presentation of two circles, followed by a fixation cross that lasted for 2000 ms while responses were recorded. The right circle was the test circle whose size was kept constant throughout the experiment. However, the size or the disparity of the left circle, i.e., the probe, changed according to the participant's response. (B) Procedure of the size adaptation experiment: Each trial started with the adaptation display, which lasted 5000 ms, followed by a 500 ms interval. The display of the test stimuli lasted for 200 ms and always contained the test and the probe. During the adaptation display, a red dot appeared on the adaptor circles for 250 ms. This appearance occurred during a random trial during every block as a detection task. After the offset of the test stimuli, participants had 2000 ms to respond.

matching tasks. The test stimulus (1.65° of visual angle; disparity, zero) was always presented at the position of the prior adaptation display (in terms of their x and y coordinates on the screen) and consequently, its perceived size was presumed to be altered by the adaptation effect. Simultaneously, a probe circle appeared opposite to the adaptor and served as a reference stimulus that was unaffected by adaptation. The size of the probe was changed according to the PEST algorithm as described above.

Additionally, during the size adaptation experiment, a second task was added: A red dot detection task served to maintain participant's attention. In this task subjects had to monitor whether a red dot appeared on the adaptor circles. The dot was presented during a random trial in every block (i.e., sixteen trials in total) for 250 ms and participants had to respond to it as fast as possible by pressing a third button using their right middle finger. After the red dot detection task, participants continued to perform the subsequent size judgment task. The trials of size judgment responses were also included in the data analysis when the dot detection task co-occurred. Neither for the size judgment nor for the red dot detection task a feedback was given.

Data analysis

The free statistical software R (R Foundation for Statistical Computing, Vienna, Austria; www.r-project.org) was used to analyze the behavioral data. The dependent variables, i.e., perceived size of the probe stimulus in the size matching task and in the size adaptation experiment, or disparity of the probe stimulus in the disparity matching task, were recorded and averaged. The size matching task allowed estimating whether subjects perceived the test and the probe stimulus at the same size. Since this was achieved without any size adaptation, a participant's potential bias to perceive the probe (which was always presented on the right side) as larger or as smaller than the test stimulus could be detected. Size estimates in size adaptation trials were corrected accordingly. The adaptation effects were then calculated as a ratio of the difference between perceived size and physical size to the physical size. A one-way ANOVA for repeated measures was conducted to assess the effects of adaptation in the different conditions. Further pairwise comparisons employing Bonferroni-correction were performed to test for specific differences between conditions. Specifically, size adaptation as induced by Large_near and Small_near adaptors was compared, in order to prove and replicate the concept that a larger adaptor generates stronger adaptation. In addition, Small_near versus Small_far and Large_near versus Large_far adaptors were contrasted in order to test whether perceived size (as altered by binocular disparity) changed size adaptation. Additionally, a comparison of adaptation effects induced by Large_near and Small_far conditions, which were matched in perceived size, was performed in order to test whether a difference in stimuli's physical size caused measurable different size adaptation effects even when perceived sizes were matched. Finally, the accuracy in detecting the red dot was calculated as the ratio of correct red dot detection trials to all red dot trials.

Results

The baseline experiment did not reveal any significant left or right side bias. Although participants perceived the size of the circle on the right side on average 1.59% smaller, this difference was not significant, $t(18) = -2.06$, $p > 0.05$.

In the disparity matching task, the individual disparity values for nineteen participants were 0.10°, 0.37°, 0.07°, 0.23°, 0.29°, 0.22°, 0.10°, 0.13°, 0.07°, 0.18°, 0.09°, 0.05°, 0.26°, 0.10°, 0.14°, 0.15°, 0.14°, and 0.11° of visual angle. The mean value of binocular disparity for nineteen participants was 0.15° of visual angle with a *SD* of 0.08. In the size adaptation experiment, the mean red dot detection rate was 97% with a *SD* of 0.11, indicating that participants paid attention to the adaptors in the adaptation period sufficiently well. The mean changes in perceived size due to adaptation after baseline correction were: 4.55% for Large_near with a *SD* 0.04, 2.89% for Small_near with a *SD* of 0.03, 4.25% for Large_far with a *SD* 0.04, and 3.10% for Small_far with a *SD* of 0.03 (Figure 3). A one-way ANOVA with repeated measures revealed a significant main effect of our experimental conditions, $F(3, 54) = 8.87$, $p < 0.001$. Pairwise comparisons (with Bonferroni correction) revealed significant differences between the Large_near and the Small_near condition, $p < 0.05$, thereby confirming pilot experiments, and showing that larger adaptors generated stronger adaptation effects. There were neither significant differences between Large_near and Large_far, $p > 0.05$, nor between Small_near and Small_far, $p > 0.05$, indicating that a larger perceived size did not generate stronger adaptation. However, the comparison between Large_near and Small_far adaptors, which were perceived the same with regard to size due to the binocular disparity, showed a significant difference, $p < 0.05$. The adaptor of larger retinal size generated significantly stronger adaptation effects although the perceived size was matched to the smaller adaptor.

In addition, we further calculated effect sizes (*ES*) and confidence intervals (*CI*s), respectively, to provide more information about the estimated magnitude of an effect and its precision. The *d* statistic, which provides a measure of the standardized difference between group means, was used to estimate *ES* (Dunlap, Cortina, Vaslow, & Burke, 1996):

$$d = t_{paired}\sqrt{\frac{2(1-r)}{n}} \quad (1)$$

where t_{paired} is the t score from the paired t test, r is the correlation coefficient between two groups, and n is the sample size.

The approximate width of 95% *CI*s for an effect size is:

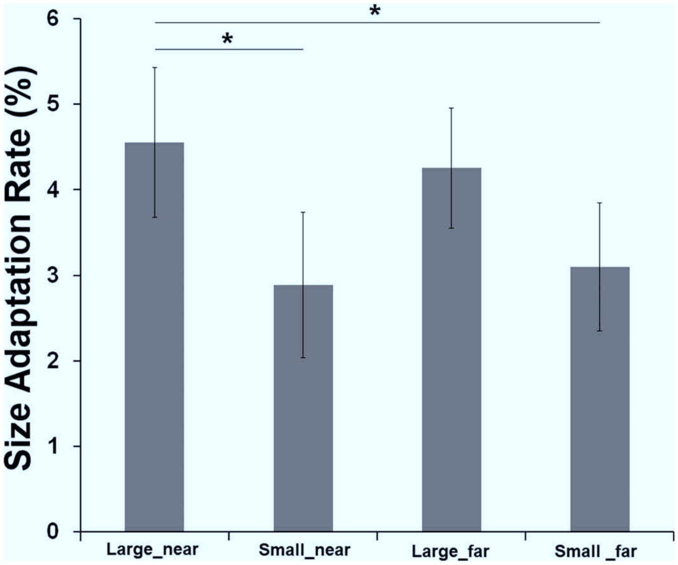

Figure 3. Behavioral results of the size adaptation experiment. Adaptation effects of the four conditions with standard errors are plotted. The mean changes in perceived size due to adaptation after baseline correction were 4.55%, 2.89%, 4.25%, and 3.10%. Pairwise comparisons (with Bonferroni correction) revealed significant differences between the Large_near and the Small_near condition, $p < 0.05$, also between the Large_near and Small_far conditions, $p < 0.05$.

$$95\%\ CI = ES - 1.96\ SE \text{ to } ES + 1.96\ SE \quad (2)$$

where ES stands for effect size (i.e., d) and SE is the asymptotic standard error for the effect size. The formulae for SE is

$$SE_d = \sqrt{\frac{2(1-r)}{n} + \frac{d^2}{2(n-1)}} \quad (3)$$

where n is the sample size and r is the correlation coefficient between two groups.

Statistic values including p values, effect sizes, and its CIs for four comparisons are reported in Table 2. Effect sizes and CIs showed similar effects as p values. The standardized differences as shown by effect sizes were larger in Large_near versus Small_near and Large_near versus Small_far comparisons. In addition, the CIs for Large_near versus Small_near and Large_near versus Small_far comparisons located beyond zero, while it included zero for Large_near versus Large_far and Small_near versus Small_far comparisons.

Experiment 2a

Binocular disparity was employed to induce depth perception in Experiment 1. In order to verify that, under the present paradigm, participants indeed had a robust depth perception with binocular disparity, we carried out a control experiment in which depth perception was assessed individually for every participant.

Methods

Participants

A new group of nine participants was enrolled in the current experiment (three female, six male; mean age 27 years old; age range, 26 to 29 years old). None of the participants reported a history of neurological or psychiatric disorders. All participants included had normal or corrected to normal vision.

Stimuli and procedure

The experimental settings were identical as those in Experiment 1. Stimuli were presented again on the LG 27MT93s 27-in 3D monitor at a distance of 66 cm. The resolution, refresh rate, and the luminance of background and stimuli were also identical to the ones in Experiment 1. Three-dimensional goggles with polarized lenses as in Experiment 1 were used to generate a 3D effect of the stimuli. The experiment comprised two parts, i.e., a disparity matching task and a depth perception experiment. Participants performed the tasks sequentially in that order.

Disparity matching task: The disparity matching task performed in Experiment 1 was conducted again in Experiment 2a to determine the individual degree of disparity required to generate adaptors with equal perceived sizes but different retinal sizes (2.7° and 2.9° of visual angle). The individual disparity values obtained were then used for a depth perception experiment. There it was tested whether participants

Statistical information	Large_near versus Small_near	Large_near versus Small_far	Large_near versus Large_far	Small_near versus Small_far
p value (pairwise comparison)	< 0.05*	< 0.05*	1.00	0.067
Effect size	0.44	0.40	0.08	0.07
CI	(0.22, 0.66)	(0.11, 0.68)	(−0.08, 0.23)	(−0.18, 0.31)

Table 2. Statistical information including p values, effect sizes and its CIs for the four comparisons in Experiment 1.

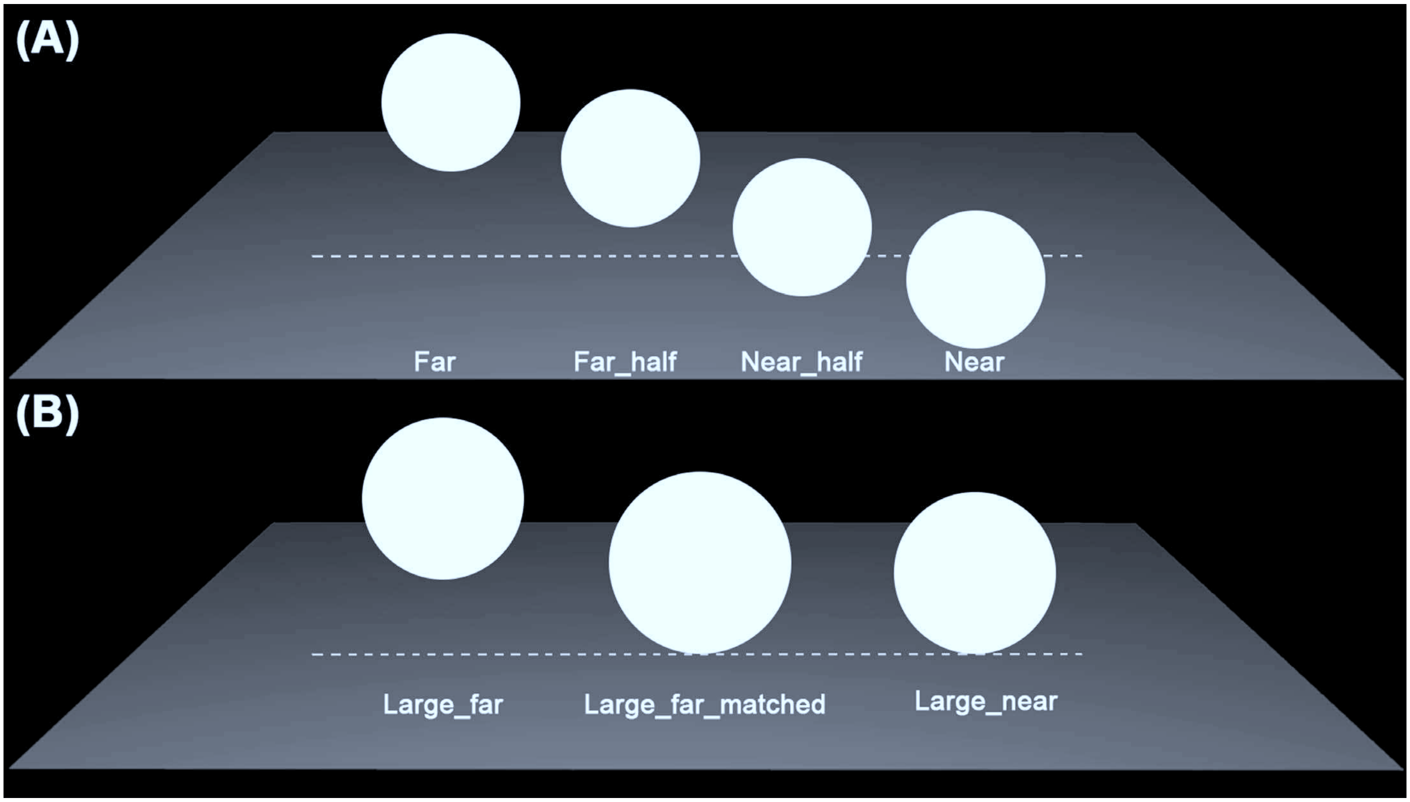

Figure 4. (A) Example of stimuli in the Depth perception experiment (Experiment 2a). The circles (2.7° of visual angle) were located at four different depth planes (i.e., Far: Z; Far_half: $Z/2$; Near_half: $-Z/2$; Near: $-Z$). Please note that the gray plane in this illustration is used only in order to exemplify depth and was not actually shown during the actual experiment where the impression of depth was created by binocular disparity. The gray dash line serves as an auxiliary line to indicate the depth plane of the screen and was also not shown during the actual experiment. (B) Example of adaptors used in Experiment 2b. In the perceived size matching task, the Large_far adaptor was set to be the standard stimulus. Its perceived size was estimated (i.e., Large_far matched adaptor) and was later used for the size adaptation experiment. In the size adaptation experiment, size adaptation effects of the Large_far matched adaptor and Large_near adaptor were measured.

were able to perceive depth with the binocular disparity derived from the disparity matching task.

Depth perception experiment: Each trial started with a 500 ms presentation of two circles (2.7° of visual angle), located to the left and to the right side, relative to the central fixation cross (2.7° of visual angle distance between the center of the circle and fixation point). The fixation cross remained at the center of the screen throughout the experiment. After stimulus presentation there was a 2000 ms time window for the participants to respond. Participants' task was to indicate with the index or ring finger of their right hand whether the left or right circle appeared further away.

The circle on the left side was presented with different disparity values. In particular, four different disparities were used and were expected to induce four different depth perceptions (Figure 4A). The disparity values used to change perceived depth were set relative to the individual disparity value Z derived from the matching task. The four values used corresponded to $\pm Z$, and half of the positive and negative value of individual disparity, $\pm Z/2$ (i.e., $-Z$, $-Z/2$, $Z/2$, Z). Positive disparities were hypothesized to create an impression of a larger distance between stimulus and observer, while negative disparities were expected to create the impression of the stimulus being closer; hence the resulting conditions are referred to as "Far", "Far_half," "Near," and "Near_half." Overall, this experiment consisted of forty trials with each depth condition comprising ten trials.

Data analysis

As in Experiment 1, in the disparity matching task of Experiment 2a the PEST algorithm was used to determine the disparity values required to match the perceived size of two stimuli with different retinal sizes. The resulting values were assessed for each subject.

In the depth perception experiment, the closer/further decisions for the different disparity values of the left circle were recorded and tested. If the disparities used in the present experiment induced a reliable depth

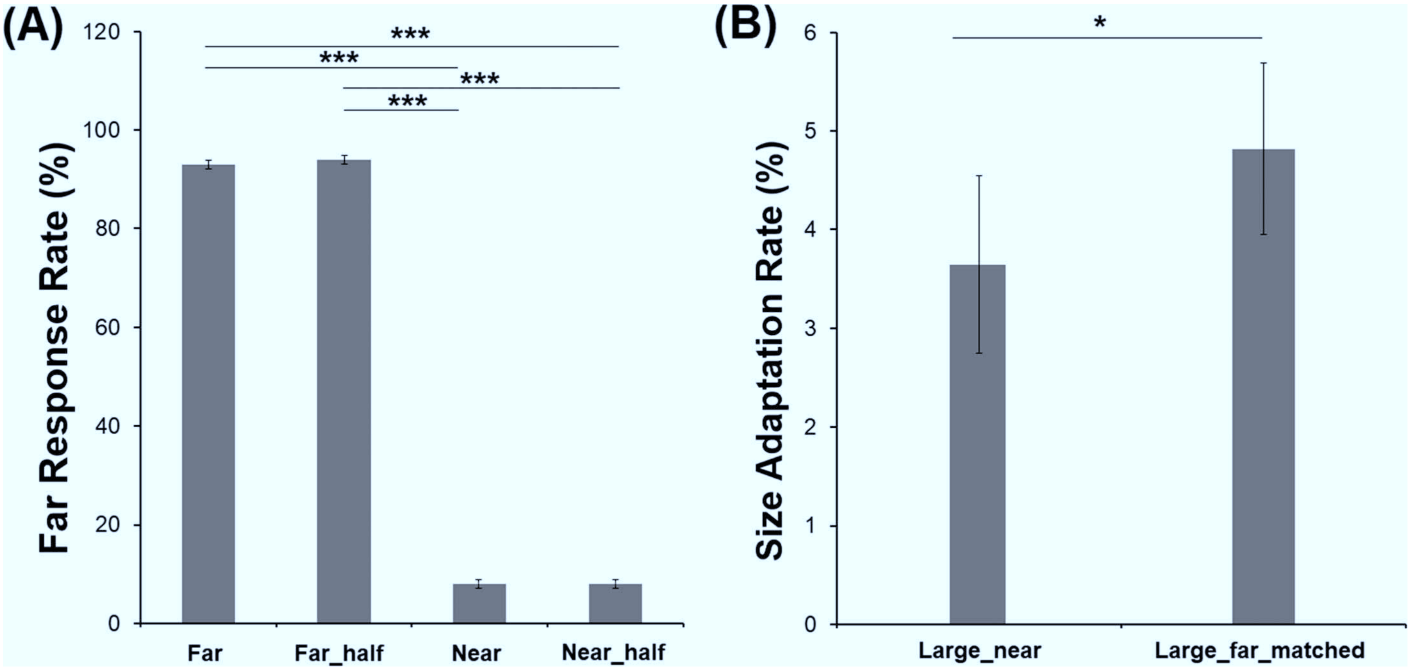

Figure 5. (A) Behavioral results of the Depth perception experiment in Experiment 2a. Far response rates of the four conditions with standard errors are plotted. Far response rates for the Far, Far_half, Near, and Near_half conditions were 93%, 94%, 8%, and 8%, respectively. Pairwise comparisons (with Bonferroni correction) revealed significant differences between the Far and Near, Far and Near_half, as well as between Far_half and Near, and Far_half and Near_half, $p < 0.001$. (B) Behavioral results of the size adaptation experiment in Experiment 2b. Adaptation effects of the two conditions with standard errors are plotted. The mean changes in perceived size due to adaptation were 3.65% and 4.82%. Paired *t* test (two-tailed) showed a significant difference between the two conditions, $t(8) = -2.63$, $p < 0.05$.

impression, then the relative amount of further decisions should be systematically biased. In particular, disparity values that increase perceived distance (i.e., Z, and $Z/2$) should increase the percentage of further decisions while disparity values that decrease perceived stimulus distance (i.e., $-Z$, and $-Z/2$) should decrease the relative amount of further responses. A one-way ANOVA with the different disparity levels as levels was conducted to determine a significant effect of disparity on perceived depth.

Results

On average, binocular disparity for nine participants was 0.44° of visual angle with a *SD* of 0.38. Individual disparity values for the nine participants were 0.51°, 0.11°, 0.35°, 1.37°, 0.19°, 0.22°, 0.30°, 0.57°, and 0.30° of visual angle.

In the depth perception experiment, the mean further decisions for the left circle for Far, Far_half, Near, and Near_half conditions were 93% with a *SD* of 0.10, 94% with a *SD* of 0.10, 8% with a *SD* of 0.09, and 8% with a *SD* of 0.04, respectively. A one-way ANOVA involving disparity values as levels revealed a significant main effect of disparity, $F(3, 24) = 493.86$, $p < 0.001$. Pairwise comparisons (with Bonferroni correction) revealed significant differences between the Far and Near, Far_ and Near_half, as well as between Far_half and Near, and Far_half and Near_Half all *p*s < 0.001 (Figure 5A).

Experiment 2b

In Experiment 1, we compared Large_near and Large_far conditions to test whether changes in perceived size significantly altered size adaptation. This test was based on the assumption that manipulations of binocular disparity altered an adaptor's perceived distance and in this context its perceived size. In particular, despite the identical retinal size of the adaptors in the Large_near and the Large_far condition, the latter was assumed to be perceived larger due to its larger distance. The test whether perceived size critically affects size adaptation depends on the magnitude of perceived size changes. In principle, the difference in perceived size may have been too small to generate any significantly different aftereffects. To rule out this possibility, we carried out Experiment 2b in which changes of perceived size were explicitly measured to ensure that participants indeed experienced the far adaptor as perceptually larger than the Large_near adaptor (Figure 4B).

Moreover, we verified that the difference in perceived size of the Large_near adaptor and the Large_far adaptor was in principle big enough to generate different size adaptation. This was achieved by comparing size adaptation induced by the Large_near adaptor and a second adaptor. This second adapter was set to be perceived as large as the Large_far adaptor but was located on the same (i.e., near) depth plane. Hence, the difference in perceived size originated from a real retinal size difference, which corresponds to the perceived size difference observed for the Large_near and the Large_far adaptors (Figure 4B).

Methods

Participants

Same participants as in Experiment 2a participated in Experiment 2b.

Stimuli and procedure

The experimental settings were identical to those of Experiment 1 and Experiment 2a. The experiment comprised two parts, a perceived size matching task and a size adaptation experiment. Participants performed the tasks sequentially in that order. The perceived size matching task was performed to generate adaptor stimuli that matched the perceived sizes of the adaptors in the Large_far and the Large_near conditions. Obviously, for the latter, no additional procedure was required since stimuli presented in the near depth plane did not involve any manipulation of binocular disparity. Therefore, its retinal and its perceived size were identical. In order to generate an adaptor stimulus, which was perceived as large as the Large_far adaptor but which was located in the near depth plane, a size matching task was required. More specifically, the Large_far adaptor was set to be the standard stimulus. Its perceived size was estimated by presenting another circle (i.e., the probe stimulus) at zero disparity. The size of the probe stimulus was changed according to the participants' responses until the standard stimulus and the probe stimulus were perceived as equally large.

The measured adaptor size (i.e., Large_far matched adaptor) was then used for the size adaptation experiment. In particular, its effects on size adaptation were compared to the Large_near adaptor. Any significant differences with regard to size adaption could be taken as evidence that the perceived size differences induced in Experiment 1 were in principle sufficiently large to generate differential size adaptation effects.

Perceived size matching task: In the perceived size matching task, the left circle, i.e., the test circle, was constantly shown at a physical size of 2.9° of visual angle with individual disparity derived from the disparity matching task in Experiment 2a, while the right circle, i.e., the probe, was shown at zero disparity with a physical size that varied according to subjects' responses. Subjects had to indicate via button press, which of the two circles appeared larger. As in the previous tasks, subjects were instructed to respond with the index or ring finger of their right hand whether the left or the right circle appeared larger. The physical size of the left circle changed according to the participant's responses using the same adaptive algorithm as used in the previous tasks. The PEST algorithm sequentially varied the probe's physical size in response to the participants' answers. As in the previous matching tasks, a trial started with a 500 ms presentation of two circles, one shown at the left and one at the right side of the fixation cross. The distance between the center of the circle and the fixation point was 2.7° of visual angle. The fixation cross remained at the center of the screen throughout the experiment. The two circles were followed by 2000 ms during which responses were recorded. The task consisted of four blocks; one block consisted of a minimum of five trials and a maximum of twenty trials. The exact number of trials varied based on the PEST algorithm and was determined by the speed at which the adaptive algorithm succeeded and stopped. The blocks were separated by breaks. Participants started the next block by pressing a third button.

Size adaptation experiment: The stimuli and the procedures applied in the size adaptation part of Experiment 2b were similar to the ones in Experiment 1. The only modification was that, instead of four adaptors, we only tested two different adaptors (i.e., Large_near adaptor and Large_far matched adaptor).

Data analysis

The dependent variables, i.e., perceived size of the probe stimulus in the perceived size matching task and in the size adaptation experiment, were recorded and averaged. The adaptation effects were calculated as the ratio of the difference between perceived size and physical size. Paired t tests were performed to assess the difference of adaptation effects induced by the two conditions. Finally, the accuracy in detecting the red dots was calculated as the ratio of correct red dot detection trials to all red dot trials.

Results

In the size adaptation experiment, the mean red dot detection rate was 100% with a *SD* of 0, indicating that participants paid attention to the adaptors in the adaptation period.

The sizes of the adaptor, which perceptually matched the Large_far adaptor, were at an individual level 3.10°, 3.00°, 3.12°, 2.99°, 3.03°, 3.10°, 3.03°, 3.23°, and 3.15° of visual angle, which are all larger than the Large_near adaptor (i.e., 2.9° of visual angle), suggesting that subjects indeed perceived the far adaptor larger than the near one. Furthermore, the mean changes in perceived size due to adaptation were 3.65% with a *SD* of 0.03 for the Large_near condition, and 4.82% with a *SD* of 0.04 for the perceptually matched for the Large_far condition (Figure 5B). Paired *t* test (two-tailed) showed a significant difference between the two adaptors, $t(8) = -2.63$, $p < 0.05$, suggesting that the difference in perceived size of near and far adaptor in principle was big enough to generate different size adaptation.

General discussion

The current study investigated the effects of size adaptation generated by the retinal or the perceived representation of an adaptor stimulus and relates the findings to cortical and subcortical structures visual information processing. Whereas the latter question could in principle be answered by testing the interocular transfer of size adaptation, the former requires an experimental manipulation of an adaptor's retinal and perceived size. We hypothesized that if size adaptation is mainly driven by a stimulus' retinal size representation in the human visual system, then adaptors of the same retinal size, i.e., independent of how large they appear, would induce similar size adaptation. Alternatively, if size adaptation is mainly driven by an adaptor's apparent size, then a similar degree of size adaptation is expected when adaptors are perceived equally large (i.e., regardless of whether they stimulate differently sized areas on the retina). Our data from Experiment 1 strongly support the first hypothesis. On one hand, retinally larger adaptors led to stronger size adaptation effects than smaller adaptors, even when their apparent size was carefully matched by adjusting their perceived distance. On the other hand, adaptors of larger apparent size did not cause stronger size adaptation effects when matched in physical size. Accordingly, the data from the present experiment clearly show that size adaptation depends on an adaptors' retinal size but is unchanged by its perceived size. Additionally, Experiment 2a demonstrated that participants indeed experienced robust depth perception as induced by binocular disparity. Furthermore, binocular disparity could be demonstrated to change perceived size. In particular, a large adaptor (2.9° of visual degree) was perceived larger when perceived further away. Moreover, we verified that the difference in perceived size of Large_near and Large_far adaptors was in principle big enough to generate different size adaptation. In contrast to adaptation of other visual features (Aslin et al., 2004), size adaptation transferred between different depth planes. Robust adaptation was observed for the Large_far and Small_far conditions where adaptors were located at the far plane, while the test stimuli were located at the near plane. Hence, from the current findings we can conclude that size adaption transferred between depth planes and that this variant of size adaptation operates on the basis of retinal representations rather than perceived size representations. Please note that in the current experiment, variations of perceived size were induced by changes of binocular disparity and hence by changes of perceived depth. Size adaptation mechanisms that are specific for a given depth plane (i.e., that do not transfer between near and far locations) cannot easily be investigated with the current experimental paradigm. However, adaptation was not found to be stronger in conditions where adaption occurred within a depth plane as compared to conditions where adaptation transferred between depth planes, suggesting a limited impact for depth plane specific adaptation.

These results allow inference with regard to the functional neuroanatomy underlying size adaptation. Perceived size is known to be coded relatively early in the human visual system. Particularly, V1 has been demonstrated to host perceived size representations (Fang et al., 2008; Murray et al., 2006; Schwarzkopf et al., 2011; Sperandio, Chouinard, et al., 2012; Weidner et al., 2014). In the present experiment binocular disparity was successfully used to generate a depth effect, which in consequence altered the stimuli's perceived size. However, the present data illustrate that size adaptation was unaffected by such changes in binocular disparity and the resulting changes in perceived size. Thus, the neural populations underlying size adaptation are most likely to be found in brain regions that are similarly blind to disparity as is the size adaptation effect. This is certainly not the case for neurons in or beyond V1, the latter being the first site at which single neurons can be activated by stimuli in both eyes (Cumming & DeAngelis, 2001).

In particular, binocular disparity has been demonstrated to be coded already in V1 (Cumming & Parker, 1999, Neri et al., 2004, Trotter, Celebrini, & Durand, 2004). It is a matter of debate whether neurons in V1 are tuned for the relative disparity, which is essential for calculating an object's perceived depth, or only to absolute disparity. While Cumming and Parker (1999) could not find any evidence for relative disparity coding in V1 during single-cell recordings in awake monkeys, Neri et al. (2004) reported effects of relative and absolute disparity already in V1 in a series of fMRI experiments. Nevertheless, irrespective of whether perceived size changes are modulated by signals that originate from V1, V2, or higher visual regions (e.g., via relative disparity) the consequence (i.e., an altered size representation) is known to be represented in V1. Although direct evidence showing that V1 reacts to the perceptual change of size derived from binocular disparity is missing, there is solid evidence that changes in perceived size induced by different types of visual illusions (and hence by different source regions in the brain) alter retinotopic representations already in human V1 (Fang et al., 2008; Kreutzer et al., 2015; Murray et al., 2006; Sperandio, Chouinard, et al., 2012; Weidner et al., 2014). Our data indicate that these altered retinotopic representations in V1 were without any relevance with regard to size adaptation. In other words, V1 *reacts* to perceived size changes (e.g., generated by size adaptation), but it is not *involved* in generating them. However, whereas our data suggest a subcortical process of size adaptation, this interpretation does not necessarily conflict with previous findings emphasizing the role of cortical regions. Rather this suggests a reinterpretation regarding their causal role at least for size adaptation as observed in the present experiment.

Overall, our data suggest that size adaptation emerges from earlier, subcortical levels of the visual processing hierarchy where information from both eyes is still coded in separate channels, such as the lateral geniculate nucleus (LGN) of the thalamus. The LGN constitutes the next lower level of visual processing. Information coming from the ipsilateral and contralateral retina is coded separately in different layers (ipsilateral layers: 2, 3, and 5; contralateral layers: 1, 4, and 6). The LGN receives information from the retinal ganglion cells via the optical nerve, the optical chiasma, and the optical tract including a number of signal transformations via retino-geniculate synapses (Saalmann & Kastner, 2011). The LGN codes visual information in retinotopic coordinates and contains retinotopic maps of the contralateral visual field. Although most of the cells in LGN show binocular interactions to some degree, they are insensitive to retinal disparity as a depth cue (Xue, Ramoa, Carney, & Freeman, 1987). Its retinotopic organization together with its insensitivity to binocular disparity renders LGN the most likely candidate region for the origin of size adaptation. In addition, LGN receives feedback from cortical regions including V1 and can be modulated by top-down mechanisms (O'Connor, Fukui, Pinsk, & Kastner, 2002), accounting for the finding that attention was found to successfully modulate size adaptation (Kreutzer et al., 2015). In sum, the results of the present experiment support the idea that LGN plays a major role in generating size adaptation. The present data indicate that the causal effects underlying size-adaptation are based on retinal size representations, presumably located in the lateral geniculate nuclei. As a consequence, an adapted stimulus' perceived size is changed, hence altering perceived size representations all along the hierarchies of the visual system. The latter may be easier to detect using fMRI since LGN is relatively small and located deep in the brain. It may, therefore, have been missed in previous fMRI studies using whole brain imaging. An involvement of LGN may account for the finding that the effects of size adaptation are associated with changes in activation of V1 (Pooresmaeili et al., 2013). LGN directly projects to V1 so activation changes in LGN will directly affect neuronal activation changes in V1.

In sum, the present findings suggest that size adaptation is based on retinal size rather than perceived size representations as induced by binocular disparity. The mechanisms underlying size adaptation seem to be unaffected by binocular disparity and are therefore most likely to be located in subcortical parts of the visual pathway, presumably the LGN.

Keywords: size perception, apparent size, visual illusions, 3D stimuli, sensory adaptation

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References

Aslin, R. N., Battaglia, P. W., & Jacobs, R. A. (2004). Depth-dependent contrast gain-control. *Vision Research*. *44*(7), 685–693.

Blakemore, C., & Sutton, P. (1969, Oct 10). Size adaptation: A new aftereffect. *Science*, *166*(3902), 245–247, doi:10.1126/science.166.3902.245.

Cohen, L. H., & Lindley, S. B. (1938). Studies in vibratory sensibility. *American Journal of Psychology*, *51*(1), 44.

Cumming, B. G., & DeAngelis, G. C. (2001). The physiology of stereopsis. *Annual Review of Neuroscience*, *24*, 203–238.

Cumming B. G., & Parker A. J. (1999). Binocular neurons in V1 of awake monkeys are selective for absolute, not relative, disparity. *Journal of Neuroscience 19*, 5602–5618.

Dalton, P. (2000). Psychophysical and behavioral characteristics of olfactory adaptation. *Chemical Senses*, *25*(4), 487–492.

Dix, M. R., Hallpike, C. S., & Hood, J. D. (1949). Auditory adaptation in the human subject. *Nature*, *164*, 59–60.

Dunlap, W. P., Cortina, J. M., Vaslow, J. B., & Burke, M. J. (1996). Meta-analysis of experiments with matched groups or repeated measures designs. *Psychological Methods*, *1*(2), 170–177.

Fang, F., Boyaci, H., Kersten, D., & Murray, S. O. (2008). Attention-dependent representation of a size illusion in human V1. *Current Biology*, *18*(21), 1707–1712.

Fisher, G. H. (1968). Illusions and size-constancy. *American Journal of Psychology*, *81*(1), 2–20.

Gilinsky, A. S. (1951). Perceived size and distance in visual space. *Psychological Review*, *58*(6), 460–482.

Goble, A. K., & Hollins, M. (1993). Vibrotactile adaptation enhances amplitude discrimination. *The Journal of the Acoustical Society of America* , *93*(1), 418–424.

Hollins, M., Washburn, S., & Bensmaïa, S. J. (2001). Vibrotactile adaptation impairs discrimination of fine, but not coarse, textures. *Somatosensory & Motor Research*, *18*(4), 253–262.

Kohn, A. (2007). Visual adaptation: Physiology, mechanisms, and functional benefits. *Neurophysiology*, *97*(5), 3155–3164.

Kreutzer, S., Fink, G. R., & Weidner, R. (2015). Attention modulates visual size adaptation. *Journal of Vision*, *15*(15):10, 1–9, doi:10.1167/15.15.10. [PubMed] [Article]

Macmillan, N. A., & Creelman, C. D. (1991). Adaptive methods for estimating empirical thresholds. In B. Webber (Ed.), *Detection theory: A user's guide* (pp. 183–209). Mahwah, NJ: Lawrence Erlbaum Associates, Inc.

Murray, S. O., Boyaci, H., & Kersten, D. (2006). The representation of perceived angular size in human primary visual cortex. *Nature Neuroscience*, *9*(3), 429–434.

Neri, P., Holly, B., & Heeger, D. J. (2004). Stereoscopic processing of absolute and relative disparity in human visual cortex. *Journal of Neurophysiology*, *92*, 1880–1891.

O'Connor, D. H., Fukui, M. M., Pinsk, M. A., & Kastner, S. (2002). Attention modulates responses in the human lateral geniculate nucleus. *Nature Neuroscience*, *5*(11), 1203–1209.

O'Mara, S., Rowe, M. J., & Tarvin, R. P. (1988). Neural mechanisms in vibrotactile adaptation. *Journal of Neurophysiology*, *59*(2), 607–622.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*(1), 97–113.

Oruç, I., & Barton, J. J. S. (2011). Adaptation improves discrimination of face identity. *Proceedings of the Royal Society of London B: Biological Sciences*, *278*(1718), 2591–2597.

Pooresmaeili, A., Arrighi, R., Biagi, L., & Morrone, M. C. (2013). Blood oxygen level-dependent activation of the primary visual cortex predicts size adaptation illusion. *The Journal of Neuroscience*, *33*(40), 15999–16008.

Qian, N. (1997). Binocular disparity and the perception of depth. *Neuron*, *18*(3), 359–368.

Saalmann, Y. B., & Kastner, S. (2011). Cognitive and perceptual functions of the visual thalamus. *Neuron*, *71*(2), 209–223.

Schwarzkopf, D. S., Song, C., & Rees, G. (2011). The surface area of human V1 predicts the subjective experience of object size. *Nature Neuroscience*, *14*(1), 28–30.

Solomon, S. G., Peirce, J. W., Dhruv, N. T., & Lennie, P. (2004). Profound contrast adaptation early in the visual pathway. *Neuron*, *42*(1), 155–162.

Sperandio, I., Chouinard, P. A., & Goodale, M. A. (2012). Retinotopic activity in V1 reflects the perceived and not the retinal size of an afterimage. *Nature Neuroscience*, *15*(4), 540–542.

Sperandio, I., Lak, A., & Goodale, M. A. (2012). Afterimage size is modulated by size-contrast illusions. *Journal of Vision*, *12*(2):18, 1–10, doi:10.1167/12.2.18. [PubMed] [Article]

Trotter, Y., Celebrini, S., & Durand, J. B. (2004). Evidence for implication of primate area V1 in neural 3-D spatial localization processing. *Journal of Physiology, Paris*, *98*(1–3), 125–134.

Weidner, R., Plewan, T., Chen, Q., Buchner, A., Weiss, P. H., & Fink, G. R. (2014). The moon illusion and size–distance scaling—evidence for shared neural patterns. *Journal of Cognitive Neuroscience*, *26*(8), 1871–1882.

Westerman, L. A., & Smith, R. L. (1984). Rapid and short-term adaptation in auditory nerve responses. *Hearing Research*, *15*(3), 249–260.

Xue, J. T., Ramoa, A. S., Carney, T., & Freeman, R. D. (1987). Binocular interaction in the dorsal lateral geniculate nucleus of the cat. *Experimental Brain Research*, *68*(2), 305–310.