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Effects of aging on biological motion discrimination

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ABSTRACT

Previous studies have shown that older subjects have difficulties discriminating the walking direction of point-light walkers. In two experiments, we investigated the underlying cause in further detail. In Experiment 1, subjects had to discriminate the walking direction of upright and inverted point-light walkers in a cloud of randomly moving dots. In general, older subjects performed less accurately and showed an increased inversion effect. Nevertheless, they were as accurate as young subjects for upright walkers during training, in which no noise was added to the display. These results indicate that older subjects are less able to extract relevant information from noisy displays. In Experiment 2, subjects discriminated the walking direction of scrambled walkers that primarily contained local motion information, random-position walkers that primarily contained global form information, and normal point-light walkers that contained both kinds of information. Both age groups performed at chance when no global form information was present in the display but were equally accurate for walkers that only contained global form information. However, when both local motion and global form information were present in the display, older subjects were less accurate then younger subjects. Older subjects again exhibited an increased inversion effect. These results indicate that both older and younger subjects rely more on global form than local motion to discriminate the direction of point-light walkers. Also, older subjects seem to have difficulties integrating global form and local motion information as efficiently as younger subjects.

1. Introduction

Aging diminishes performance in a variety of visual domains including object recognition (Boutet & Faubert, 2006; Kessels, Hobbel, & Postma, 2007), colour vision (Fiorentini, Porciatti, Morrone, & Burr, 1996), and binocular integration (Alvarez, Puell, Sanchez-Ramos, & Villena, 2006). But perhaps the best-studied age-related deficits are in motion perception (Andersen & Ni, 2008; Atchley & Andersen, 1998; Bennett, Sekuler, & Sekuler, 2007; Gilmore, Wenk, Naylor, & Stuve, 1992; Norman, Ross, Hawkes, & Long, 2003; Snowden & Kavanagh, 2006; Trick & Silverman, 1991). For example, previous researchers have found age-related deficits in direction and speed discrimination (Atchley & Andersen, 1998; Bennett et al., 2007; Gilmore et al., 1992; Norman et al., 2003; Snowden & Kavanagh, 2006; Trick & Silverman, 1991), collision detection (Andersen, Cisneros, Saidpour, & Atchley, 2000; Andersen & Enriquez, 2006), shape from motion (Blake, Rizzo, & McEvoy, 2008; Norman, Bartholomew, & Burton, 2008; Norman, Clayton, Shular, & Thompson, 2004; Norman et al., 2006; Norman, Dawson, & Butler, 2000; Wist, Schrauf, & Ehrenstein, 2000) and second-order motion perception (Habak & Faubert, 2000). The current study extends research within the domain of motion perception to determine whether similar effects of aging occur for high-level motion tasks using biologically relevant motion stimuli, specifically point-light walkers.

Point-light walkers are useful stimuli for studying motion because their local elements have properties that are similar to random dot stimuli used in most of the studies mentioned above, but, in addition, they have a high-level interpretation of a moving person that is achieved by grouping the local elements into a global form. Biological motion perception was first demonstrated by Johansson (1973). He attached point-lights to the joints of a moving person and showed that those were enough to perceive the human figure. Empirical studies demonstrated that such point-light walkers convey information about identity (Cutting & Kozlowski, 1977), sex (Kozlowski & Cutting, 1977), and emotional state (Dittrich, Troscianko, Lea, & Morgan, 1996; Roether, Omlor, & Giese, 2008). It is also possible to identify actions performed by point-light walkers (Vanrie & Verfaillie, 2004). Local motion information seems to be essential to perceive those characteristic attributes of a walker or its performed actions, and it has been assumed that point-light walkers are primarily analyzed using its local motion characteristics (Mather, Radford, & West, 1992). But more recently it has been shown it is still possible to perceive biological motion

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when the walker is presented in a cloud of random dots that mask the local image motion of the walker (Bertenthal & Pinto, 1994), and even in the absence of local image motion, observers can readily recognize biological motion from point-light displays (Beintema & Lappe, 2002). These results indicate that both local motion and the global form of the walker are important to recognize biological motion.

Two previous studies have shown that the perception of point-light walkers is impaired in some way in older subjects (Billino, Bremmer, & Gegenfurtner, 2008; Norman, Payton, Long, & Hawkes, 2004). Norman, Payton, et al. (2004) studied subjects' performance for recognizing apparent motion displays of point-light walkers that were walking, jogging, or skipping. Older subjects were significantly impaired for walkers that were presented for a short stimulus duration and stimuli that were partly occluded. In another study, Billino et al. (2008) showed that older subjects were less able to detect walkers that were presented in a cloud of randomly moving dots with limited life time. Although the studies by Billino et al. (2008) and Norman, Payton, et al. (2004) both demonstrated that older subjects have greater difficulty perceiving point-light walkers, the question remains as to what kind of mechanisms produce the age-related deficits. The question is especially intriguing given that the effect of aging on the perception of point-light walkers is small compared to the effects of aging on other motion perception tasks, especially low-level motion perception (Billino et al., 2008). Therefore, investigating the mechanisms underlying age-related decline in biological motion perception might shed light on the general mechanisms underlying motion perception in the aging brain.

One possible explanation of the age difference in the perception of point-light walkers is that older subjects are less able to encode the local motion properties of the walker. This hypothesis is consistent with psychophysical studies showing age-related deficits in low-level motion perception (Bennett et al., 2007; Gilmore et al., 1992; Roudaia, Pilz, Sekuler, & Bennett, 2009; Snowden & Kavanagh, 2006; Trick & Silverman, 1991), and with physiological studies showing age-related reductions in the speed selectivity of MT neurons (Yang et al., 2009) and/or changes in the response properties of V1 and V2 neurons (Leventhal, Wang, Pu, Zhou, & Ma, 2003; Schmolesky, Wang, Pu, & Leventhal, 2000; Yu, Wang, Li, Zhou, & Leventhal, 2006) that project to MT. Another possibility is that older subjects are less able to group the local elements of the walker into a coherent global form. It has been shown, for example, that older subjects are sometimes less able to integrate information across space (Andersen & Ni, 2008; Del Viva & Agostini, 2007; Roudaia, Bennett, & Sekuler, 2008; Roudaia et al., 2009; Salthouse, 1987). Therefore, older subjects might be impaired in processing walkers because they are less able to perceive the global form of the walker. Of course, deficits in both local and global processing could contribute to impaired perception of biological movements.

The two experiments described here examined the contributions of local and global deficits to the age-related decline in in the perception of point-light walkers. In both experiments subjects had to judge the walking direction of point-light walkers. In Experiment 1, walkers were presented in a random noise mask similar to the one used by Billino et al. (2008). In Experiment 2, walkers were presented without noise. To investigate whether older and younger subjects rely on different sources of information to discriminate the direction of point-light walkers, we used three different kinds of walkers: normal walkers, which contain both local motion and global form information; scrambled walkers which lack global form information; and random-position walker, which lack local motion information. It has been suggested that stimulus inversion alters the processing of global form for the recognition of biological motion (Pavlova & Sokolov, 2000; Sumi, 1984; Troje & Westhoff, 2006), and therefore both experiments measured performance with upright and inverted walkers.

2. Experiment 1

In Experiment 1, subjects discriminated the walking direction of point-light walkers presented in a dynamic random-noise mask. Billino et al. (2008) demonstrated an age-related decline in detecting point-light walkers presented for 400 ms. However, Norman, Payton, et al. (2004), who investigated discrimination performance for occluded walkers, found that older subjects' performance increased with longer stimulus durations. Therefore, Experiment 1 included a large range of durations (0.08–3.2 s), and examined the extent to which the presentation time of the walker differentially affected the perception of biological motion in younger and older subjects. It has been suggested that stimulus inversion alters the processing of global form, or spatial relations among features, for both face recognition (Maurer, Grand, & Mondloch, 2002; Tanaka & Farah, 1991; but see Gaspar, Bennett, & Sekuler, 2008 and Sekuler, Gaspar, Gold, & Bennett (2004)) and the recognition of biological motion (Pavlova & Sokolov, 2000; Sumi, 1984; Troje & Westhoff, 2006). If this hypothesis is correct, and if older and younger subjects differ in the extent to which they rely on global form to discriminate the direction of point-light walkers, then we would expect stimulus inversion to affect performance differently in older and younger subjects. Therefore, Experiment 1 measured direction discrimination with both upright and inverted point-light walkers.

Previous studies have shown that older women have higher motion thresholds than older men and younger adults (Gilmore et al., 1992; Trick & Silverman, 1991) and are less sensitive to motion information involving optic flow (Andersen & Atchley, 1995; Atchley & Andersen, 1998). This age-related sex difference has not been addressed previously in the context of biological motion, and therefore we included sex as a variable in the current study.

2.1. Methods

2.1.1. Subjects

Twelve younger subjects ($M = 21.9$ years; Range = 18–28; six male) and 12 older subjects ($M = 71.0$ years; Range = 61–78; six male) took part in the experiment. All subjects were naïve as to the purpose of the experiment, and all had normal or corrected-to-normal visual acuity. A general health questionnaire was administered prior to testing, and none of the subjects reported having any visual disorders or major health problems. All subjects had visited an ophthalmologist or an optometrist within the past three years and were free of glaucoma, strabismus, amblyopia, macular degeneration, and cataracts. None of the subjects was aphakic. Older subjects also completed the Mini-Mental State Examination (Folstein, Folstein, & McHugh, 1975) to assess their cognitive abilities. All scores were within the normal ranges for subjects, age and education levels (Crum, Anthony, Bassett, & Folstein, 1993). Subjects were paid $10/h for their participation in the experiment.

2.1.2. Stimuli

Point-light walker stimuli were generated using a modified version of Cutting's classic point-light walker algorithm (Cutting, 1978; Thornton, Pinto, & Shiffrar, 1998; Thornton, Vuong, & Bülthoff, 2003). The walker did not translate across the screen, but rather appeared to walk in place as if on a treadmill. The animated walker consisted of 11 dots that simulated points on the head, near the shoulder, both elbows, both wrists, the hip, both knees and both ankles. To increase task difficulty, the walker was occluded by a mask that consisted of 44 dots whose positions varied randomly on each frame. Walker and mask dots were identical in size and contrast, and could be discriminated from one another only by their motion characteristics. The walker figure subtended

$1.9^{\circ} \times 4.2^{\circ}$. The position of the walker was randomized within the noise mask so that the walker was displaced by up to 0.75° visual angle in any direction from the middle. In addition, the starting point of the stride cycle was chosen randomly on every trial. This randomization procedure prevented subjects from recognizing the walker simply from the starting position on the screen or from a specific animation frame. Walkers were presented at a frame rate of 25 fps, and a complete stride cycle was achieved after 40 frames, or 1.6 s.

2.1.3. Apparatus

The experiment was conducted on a Macintosh G4 computer (OSX) under the control of the Video and Psych ToolBox extensions for MATLAB (Brainard, 1997; Pelli, 1997). Stimuli were presented on a 19 in Apple Studio Display (model M6204), with a resolution of 1024×864 pixels and a refresh rate of 75 Hz.

2.1.4. Procedure

Each subject was seated in a darkened room, and viewed the stimuli binocularly with a chin/forehead rest stabilizing the subject's head at a distance of 60 cm from the screen. On each experimental trial, subjects saw a side-view of a point light walker presented in a cloud of 44 noise dots. The walker's direction of motion was either rightward or leftward, and the walker was either presented upright or inverted. Stimulus duration was 2, 5, 10, 20, 30, 40 or 80 frames (0.08–3.2 s). Each subject performed 20 trials per stimulus duration, resulting in a total of 280 trials. All conditions (2 orientations $\times$ 7 durations) were randomly intermixed for each subject. On each trial, subjects had to decide whether the walker was walking towards their left or right by pressing a button on a standard computer keyboard. Prior to the start of the main experiment, each subject completed two blocks – one for upright point-light walkers and another for inverted – of 20 practice trials for stimuli presented without noise dots for 40 frames.

2.2. Results

Fig. 1 shows response accuracy for older and younger subjects at all stimulus durations for upright and inverted walkers. An analysis of variance (ANOVA) on arcsin-transformed data showed that, across all conditions, older subjects performed considerably worse than younger subjects ($F(1,20) = 109.97,\ p < 0.001$). In addition, both age groups exhibited a clear inversion effect: response accuracy was significantly greater for upright than inverted walkers ($F(1,20) = 34.13,\ p < 0.001$). There also was a main effect of stimulus duration ($F(6,120) = 107.24,\ p < 0.001$) – both older and younger subjects performed better at longer presentation times. An age $\times$ stimulus duration interaction showed that accuracy increased more slowly with increasing stimulus duration in older than younger subjects ($F(6,120) = 12.64,\ p < 0.001$). The analysis also revealed an age $\times$ stimulus orientation $\times$ stimulus duration interaction ($F(6,120) = 2.39,\ p < 0.05$): for younger subjects, the difference between accuracy in the upright and inverted conditions decreased as stimulus duration increased, but in older subjects the upright-inverted difference actually increased at longer stimulus durations. This three-way interaction is due to (i) a floor effect on the performance of older subjects in the inverted condition at short durations; and (ii) a ceiling effect on the performance of younger subjects in the upright condition at long durations.

Fig. 2, which plots results from male and female subjects separately, indicates that older females performed significantly worse than older males at longer stimulus durations, whereas younger females performed worse than younger males at shorter stimulus durations. Also, the effect of stimulus duration was significantly smaller in older female subjects. These observations were confirmed by an ANOVA, which found a significant three-way interaction between age, stimulus duration, and sex ($F(6,120) = 3.37,\ p < 0.01$). The effect of noise on performance is illustrated in Fig. 3, which shows accuracy obtained by older and younger subjects with stimulus durations of 40 frames in the practice and

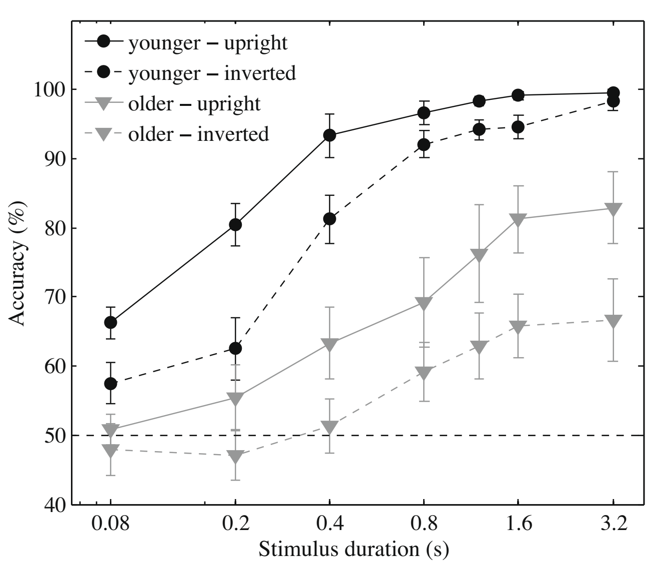

Fig. 1. Response accuracy from Experiment 1 for older and younger subjects at all stimulus durations for upright and inverted walkers. Error bars represent standard errors of the mean (SEM).

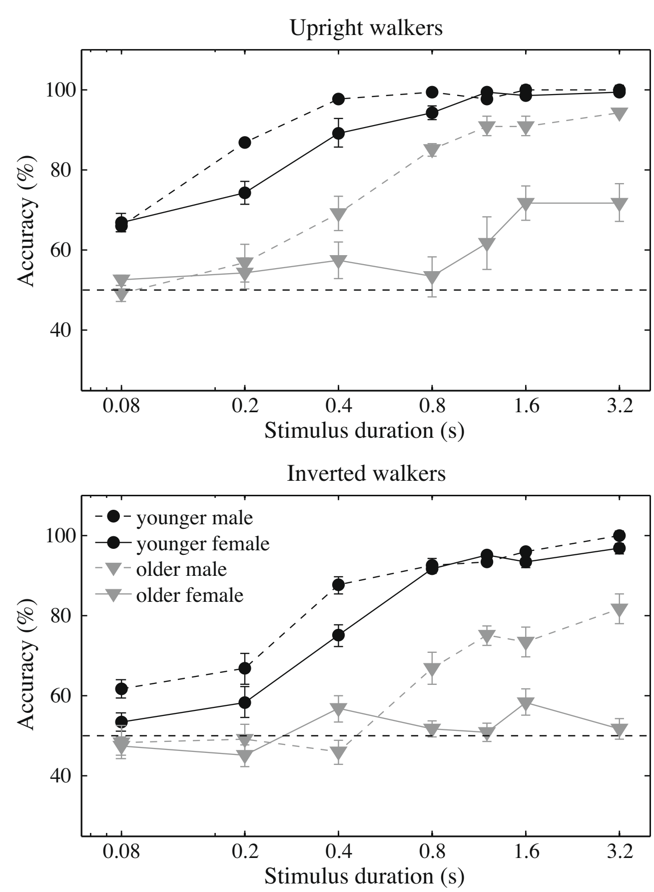

Fig. 2. Response accuracy from Experiment 1 for female and male older and younger subjects at all stimulus durations for upright walkers (top) and inverted walkers (bottom). Error bars represent SEM.

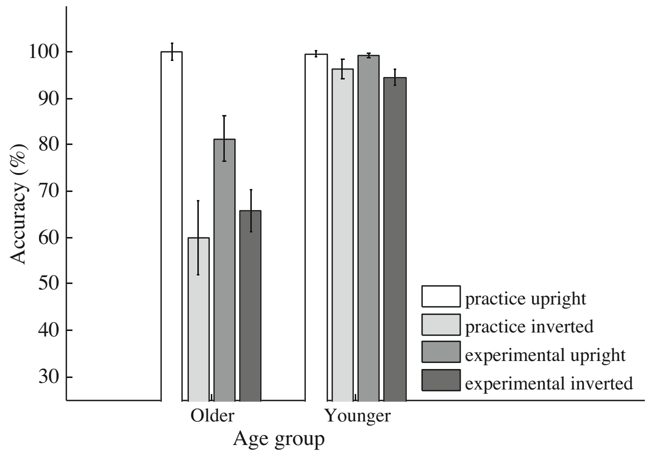

Fig. 3. Response accuracy from Experiment 1 for older and younger subjects for upright and inverted walkers at 40 frames during practice (without noise) and experimental blocks (with noise). Error bars represent SEM.

experimental blocks, which used stimuli with and without noise, respectively. An ANOVA on arcsin-transformed data revealed significant main effects of stimulus orientation ($F(1,20) = 20.19,\ p < 0.001$) and age ($F(1,20) = 41.08,\ p < 0.001$), indicating that performance in both age groups was better with upright than inverted walkers, and that performance was worse in older subjects than younger subjects. However, there also was a significant age $\times$ noise interaction ($F(1,20) = 9.65,\ p < 0.001$), which reflected the fact that the difference between age groups was greater in conditions that used noise. An age $\times$ stimulus orientation interaction was only marginally significant ($F(1,20) = 3.77,\ p = 0.066$).

2.3. Discussion

The results of the current experiment replicate previous reports that older subjects are less able to discriminate the walking direction of point-light walkers presented in noise (Billino et al., 2008). As shown by Norman, Payton, et al. (2004) with occluded walkers, the difference between age groups decreased at long stimulus durations. Nevertheless, unlike the experiment by Norman, Payton, et al. (2004), older subjects never reached the same performance level as younger subjects in the current experiments: older subjects – particularly older females – were significantly worse than younger subjects even at the longest stimulus durations tested. The fact that the upper asymptote of performance was lower in older subjects implies that the observed age differences in performance are not due entirely to slower processing by the senescent visual system (Salthouse, 1996).

We found that the effect of age was increased for inverted walkers. Inversion is thought to disrupt the perception of the global form of a walker (Pavlova & Sokolov, 2000; Sumi, 1984; Troje & Westhoff, 2006). If inversion specifically impairs the perception of the global stimulus configuration, then the observation that the inversion effect was greater in older subjects might indicate that older subjects rely more on the global form of an upright walker to discriminate its walking direction. However, some have argued that effects of stimulus inversion may not be due to a specific effect of configural processing, or the perception of global form, but rather reflects the effects of familiarity or learning on the efficiency with which viewers encode global *and* local aspects of upright and inverted stimuli (Sekuler et al., 2004; Gaspar, Bennett, et al., 2008; Gaspar, Sekuler, & Bennett, 2008). Such experience-based effects might be more pronounced in older subjects because they have greater experience with upright walkers.

Interestingly, performance in both age groups was similar for walkers presented for an extended duration without noise during training. Whereas younger subjects did not seem to be affected by noise at a stimulus duration of 40 frames, older subjects performance decreased significantly when noise was added to the display. The effect of noise on on the perception of point-light walkers for older subjects indicates that older subjects have more difficulties extracting relevant information from noisy displays, a point that we return to in the General discussion. Like previous studies on low-level motion perception, we found an age-related effect of sex (Atchley & Andersen, 1998; Snowden & Kavanagh, 2006; Gilmore et al., 1992): Female subjects showed a bigger decline in the perception of point-light walkers than male subjects. So far, there is no clear explanation for such a sex difference in older subjects, but given the variety of other tasks that show sex differences in visual motion perception (Andersen & Atchley, 1995, 1998; Gilmore et al., 1992; Trick & Silverman, 1991), older women in general seem to be more affected by visual decline in the motion pathway.

3. Experiment 2

Experiment 1 found that older subjects had greater difficulty discriminating the walking direction of point-light walkers in noise, especially when the walkers were inverted. In Experiment 2 we investigated whether this age difference was caused by older and younger subjects relying on different sources of information to estimate the direction of point-light walkers. Therefore, in addition to the normal point-light walker used in Experiment 1, Experiment 2 also used scrambled walkers and random-position walkers.

Scrambled walkers have the same local motion information as normal walkers, but their global form is obscured by randomly changing the position of the walkers' dots at the beginning of a walk sequence. It has been suggested that the local motion information of individual dots provides enough information to correctly identify the walking direction of an upright walker (Troje & Westhoff, 2006). In contrast, random-position walkers (Beintema & Lappe, 2002) – in which the position of dots change on each frame, but always remain on the body frame – do not contain coherent local dot motion, but do preserve global form information. If older subjects have more difficulties discriminating the walking direction for random-position walkers than younger subjects, it would suggest that older subjects rely more on local motion information for processing point-light walkers. If, however, older subjects are less able to discriminate the walking direction for scrambled walkers, it would suggest that older subjects rely more on global form information. Given the large effect of noise on older subjects' performance, as indicated by comparing practice and test trials in Experiment 1, here we decided to investigate performance in the absence of noise to ensure that local and global manipulations would not be confounded by age-related difficulties in processing stimuli embedded in noise.

3.1. Methods

3.1.1. Subjects

Twelve younger subjects ($M = 23$ years; Range = 19–29; six male) and 12 older subjects ($M = 69.6$ years; Range = 66–75; six male) took part in the experiment. All subjects were naïve as to the purpose of the experiment. As in Experiment 1, subjects had normal or corrected-to-normal visual acuity, all subjects were free of eye pathologies, and all subjects were paid $10/h for their participation. All subjects had visited an ophthalmologist or an optometrist within the past three years and reported that they had no known visual problems.

3.1.2. Stimuli

The stimuli were the same as those used in Experiment 1, with the following modifications: In the scrambled-walker condition, the starting vertical positions of the walker's dots were randomly selected along the vertical axis of the display so that the local dot motion, but not the underlying skeleton, was preserved. In the random-position condition, the dots were presented at random positions along the limbs of the walker so that the underlying skeleton was preserved, but not the local dot motion. The possible positions of the points on the walker's skeleton were distributed uniformly across the 10 body segments, with each segment defined by the line connecting the joints. The segments corresponded to the neck, the body, and left and right upper arm, lower arm, upper leg and lower leg. The dots were randomly repositioned on their corresponding segments on each frame (Beintema & Lappe, 2002). Finally, unlike Experiment 1, all walkers were presented without noise.

3.1.3. Apparatus

The experiment was conducted on a Macintosh G5 computer (OSX) under the control of the Video and Psych ToolBox extensions for MATLAB (Brainard, 1997; Pelli, 1997). Stimuli were presented on a 19 in Sony GDM-C520 monitor, with the same resolution and refresh rate as used in Experiment 1.

3.1.4. Procedure

Subjects discriminated the walking direction of each point-light walker. Before the start of the experiment, all subjects completed six blocks of four practice trials in the following order: upright normal walker; inverted normal walker; upright random-position walker; inverted random-position walker; upright scrambled walker; and inverted scrambled walker. In the main experiment, the type of point-light walker (i.e., normal, scrambled, and random-position) was blocked, and the order of the blocks was randomized across subjects. At the beginning of each block, subjects performed an additional set of eight practice trials (four with upright and four with inverted stimuli) with the type of walker for that block. On all practice trials, walkers were presented for 40 frames. In each block of experimental trials, walkers were presented at stimulus durations of 2, 5, 10, 20, 40, 80 and 120 frames (frame rate = 25 fps, 0.08–4.8 s). In each block, stimulus orientation and duration were randomized across trials. Each subject performed 8 trials per stimulus duration, resulting in a total of 336 trials.

3.2. Results

Fig. 4 shows response accuracy, for older and younger subjects, for each type of upright and inverted walkers at all stimulus durations. Arcsin-transformed data were analyzed initially with a 3 (walker type) × 2 (age) × 2 (sex) × 2 (orientation) × 7 (duration) ANOVA. The main effect of sex was not significant nor did it interact with any other variable, and therefore sex was dropped from subsequent analyses. A 3 (walker type) × 2 (age) × 2 (orientation) × 7 (duration) ANOVA showed that the two-way interactions between walker type and orientation ($F(2,40) = 5.83,\ p < 0.01$), age ($F(2,40) = 3.58,\ p < 0.05$), and duration ($F(12,240) = 3.99,\ p < 0.001$) were all significant, and therefore data collected with each type of walker were analyzed with separate 2 (age) × 2 (orientation) × 7 (duration) ANOVAs.

In the scrambled walker condition, response accuracy was near chance levels in all conditions and none of the main effects or interactions were significant. With random-position walkers, there were significant main effects of stimulus orientation ($F(1,22) = 19.04,\ p < 0.001$) and duration ($F(6,132) = 31.52,\ p < 0.001$), but the effect of age was not significant ($F(1,22) = 1.88,\ p = 0.18$), nor did it interact with any other variable. In the normal walker condition, there was a significant age × orientation × duration interaction ($F(6,132) = 2.88,\ p < 0.05$), and therefore data obtained with upright and inverted stimuli were analyzed separately. The ANOVA for inverted normal walkers revealed significant main effects of age ($F(1,22) = 5.85,\ p < 0.05$) and duration ($F(6,132) = 3.36,\ p < 0.01$); the age × duration interaction was not significant ($F(6,132) = 1.04,\ p = 0.40$). The ANOVA for upright normal walkers found a significant main effect of duration ($F(6,132) = 9.59,\ p < 0.001$) and a significant age × duration interaction ($F(6,132) = 2.36,\ p < 0.05$); the main effect of age was not significant ($F(1,22) = 1.33,\ p = 0.26$). The interaction between age and duration reflects the fact that older subjects had lower accuracy than younger subjects at the two shortest stimulus durations, but not at the other durations.

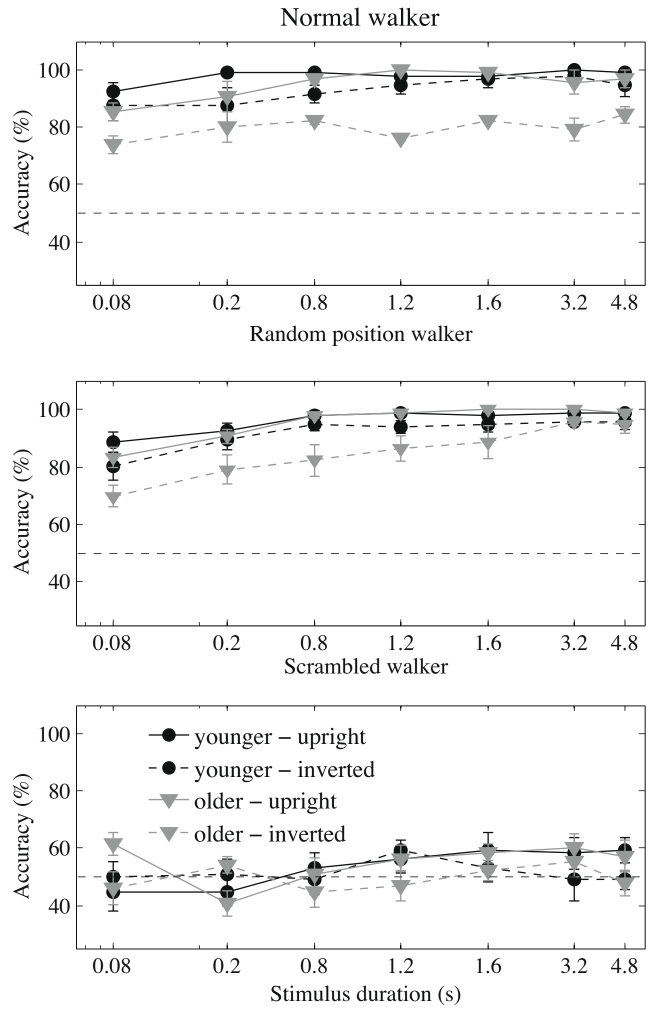

Fig. 4. Response accuracy for older and younger subjects for upright (solid lines) and inverted (dashed lines) normal (top), random-position (middle), and scrambled (bottom) walkers at various stimulus durations. Error bars represent SEM.

In summary, significant differences between older and younger subjects were obtained only with with upright normal walkers at short stimulus durations and with inverted normal walkers across a wide range of stimulus durations.

In Fig. 5 the difference between accuracy measured with normal walkers in Experiments 1 and 2 is plotted as a function of stimulus duration. Experiment 1 used noise but Experiment 2 did not, so Fig. 5 can be interpreted as showing the effect of noise on response accuracy. The figure clearly shows that, in both age groups, the effect of noise on response accuracy was strongest at short stimulus

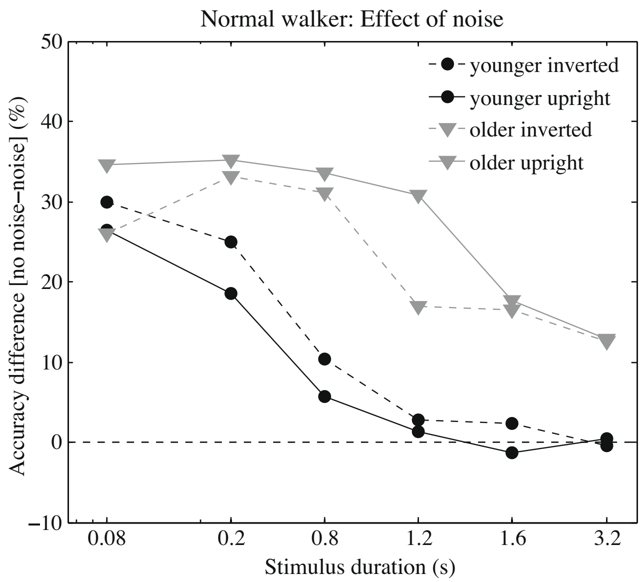

Fig. 5. The difference between response accuracy measured in Experiments 1 and 2 with normal walkers. The stimuli used in Experiment 1, but not Experiment 2, were embedded in noise, so the difference represents the effect of noise on direction discrimination accuracy. The conditions that used stimulus durations of 30 frames (in Experiment 1) and 120 frames (in Experiment 2) were not included in both experiments and therefore are not shown in the figure.

durations and declined at longer durations. However, the decline was less pronounced in older subjects, who were affected significantly by the presence of noise even at the longest stimulus durations. Hence, noise had a much greater effect on performance in older than younger subjects at stimulus durations longer than 2–5 frames (i.e., 80–200 ms). At a stimulus duration of 40 frames (i.e., 1.6 s), for example, noise had no effect on response accuracy in younger subjects but reduced accuracy in older subjects by more than 15%, a result that is similar to the one shown in Fig. 3.

3.3. Discussion

Experiment 2 found significant age differences only with normal walkers: Older subjects had more difficulties than younger subjects discriminating inverted normal walkers, and upright normal walkers at short stimulus durations. There were no age differences in the condition that used random-position walkers, in which both age groups performed well above chance with both upright and inverted walkers, or in the scrambled walker condition, in which both age groups performed at chance. A comparison of response accuracy obtained with normal walkers in Experiments 1 and 2 indicated that older subjects were affected much more than younger subjects by the presence of stimulus noise, especially at longer stimulus durations (Fig. 5). Unlike Experiment 1, the current Experiment did not find evidence of sex differences in older subjects.

In both age groups, performance for both normal and random-position walkers was above chance at all stimulus durations, whereas performance for scrambled walkers was near chance at all stimulus durations. Scrambled-walkers preserve local motion information, but disrupt global form, and therefore the near-chance performance of both age groups in that condition suggests that local information on its own is insufficient for discriminating direction. The very poor performance obtained with scrambled walkers contrasts with previous studies that reported above-chance performance for discriminating the direction of such stimuli (Troje & Westhoff, 2006). This difference between results might be due to the use of different specific examples of walkers used in the two experiments: the walkers used in the current experiments simply might have less pronounced local motion information and therefore, some form information is needed to be able to discriminate their walking direction (Saunders, Suchan, & Troje, 2009). Regardless, the present result does cast doubt on the generalizability of results from the scrambled walking paradigm.

The fact that there was no difference between age groups for random-position walkers, and accuracy was very high for both age groups, suggests that form information alone is sufficient to discriminate the walking direction of point-light walkers. The fact that older subjects performed worse in certain conditions with normal walkers, suggests that older subjects are less able to integrate form and motion information. Random-position walkers are mainly discriminable on the basis of global form information, whereas for normal walkers, subjects need to be able to integrate form and motion information to perceive the walker as a whole. Older subjects were significantly worse than younger subjects at discriminating upright walkers at short stimulus durations, which indicates that they require more time to integrate form and motion information than younger subjects.

As in Experiment 1, the inversion effect (with normal walkers) was larger in older subjects. Previous studies have linked inversion effects to the disruption of the stimulus configuration during inversion (Pavlova & Sokolov, 2000; Sumi, 1984; Troje & Westhoff, 2006). Nevertheless, the fact that the increased inversion effect for older subjects is found only with normal walkers, and not random-position walkers, makes it unlikely that the increased inversion effect is due to a general disruption of the form or stimulus configuration of the walker. Rather, older subjects seem to have more difficulties processing the additional motion information that is present in the normal walker. An increased familiarity for upright walkers might help older subjects to compensate for difficulties integrating form and motion information for upright walkers that are presented for an extended period of time, indicated by the fact that the age difference disappears at longer stimulus duration for upright normal walkers.

Unlike Experiment 1, the current Experiment did not find sex differences. One possible explanation could be that older women are more affected by noise present in the stimulus, which needs to be investigated in further detail.

4. General discussion

In two experiments we compared older and younger subjects' accuracy for discriminating the walking direction of upright and inverted point-light walkers at different stimulus durations. Experiment 1, which used walkers embedded in noise, found that younger subjects were more accurate than older subjects across stimulus durations ranging from 0.08 to 3.2 s, and that the effect of stimulus inversion was larger for older subjects. However, we did not find age differences on practice trials, which did not contain noise and had a stimulus duration of 1.6 s (i.e., 40 frames). Experiment 2 used three kinds of walkers displayed without noise: normal walkers that contained both local motion and global form information, random-position walkers that preserve global form information but disrupt local motion information, and scrambled-walkers that preserve local motion information but disrupt global form. Older subjects were as good as younger subjects at discriminating the walking direction of random-position walkers, but showed decreased performance for upright normal walkers at shorter stimulus durations and inverted normal walkers. A comparison between performance in Experiments 1 and 2 for normal walkers again found that older subjects were more affected by noise than younger subjects. Both age groups performed at chance for scrambled walkers at all stimulus durations. Overall, the results from the two experiments indicate that: (a) older subjects have difficulties extracting relevant information from noisy environments; and (b) Older subjects are less efficient at integration form and motion information than younger subjects.

Although in Experiment 1 older subjects generally had greater difficulty discriminating point-light walkers than younger subjects, the age difference cannot be attributed to some general inability on the part of older subjects to perceive point-light walkers *per se*, because there was no age difference on practice trials that did not use noise (Fig. 3). Therefore, it rather seems as if older subjects were less able to extract relevant information from the stimulus display when the walkers were presented in a random noise mask. These results were confirmed by comparing data from Experiment 1 and Experiment 2. The effect of noise was significantly higher for older subjects and, even at longer stimulus durations, older subjects never reached the performance level of younger subjects when the walkers were presented in noise. This result is consistent with Billino et al. (2008), who showed that older subjects needed a higher signal-to-noise ratio to detect point-light walkers embedded in a random noise mask. Other studies also have reported that older subjects are less able to extract information from noisy displays. For example, previous studies on the perception of shape from motion have shown that older subjects are impaired in discriminating 3D shapes using motion cues and motion parallax in the presence of noise that was defined as limited lifetime of the points forming the stimulus (Norman et al., 2000; Norman, Clayton et al., 2004). In addition, older subjects have difficulties extracting relevant information from cluttered scenes in everyday situations such as driving (Kline et al., 1992), during visual search, older subjects seem to be impaired in discriminating relevant targets from distractors as efficiently as younger subjects (Plude & Hoyer, 1986; Plude & Doussard-Roosevelt, 1989; Sekuler & Ball, 1986; Rabbitt, 1965), and experiments testing the useful field of view showed that older subjects seem to be impaired in conditions involving divided attention (Sekuler, Bennett, & Mamelak, 2000; Richards, Bennett, & Sekuler, 2006).

The failure to find an age difference with normal walkers presented without noise at longer stimulus durations is especially intriguing given older subjects' reduced ability to detect and discriminate low-level visual motion (Atchley & Andersen, 1998; Bennett et al., 2007; Billino et al., 2008; Gilmore et al., 1992; Snowden & Kavanagh, 2006; Trick & Silverman, 1991). Point-light walkers share some of the characteristics of random-dot kinematograms, which have been used to study age-related changes in low-level motion perception. However, unlike random-dot kinematograms, the local elements of point-light walkers can be grouped and organized to form the percept of a single moving object (i.e., a walking person). This high-level interpretation of the stimulus might help older subjects to perform the task. Of course, the lack of an age difference for walkers presented without noise in Experiment 1, and in Experiment 2 for upright walkers presented at extended stimulus durations, could simply reflect the fact that the task is easier than previous studies investigating low-level motion perception in aging. Accuracy for normal and random-position walkers in Experiment 2 was close to 100%, whereas in the studies mentioned above response accuracy was much lower. Interestingly, though, the inversion effect was still significantly larger in older subjects for normal walkers even when no noise was presented in the display (Fig. 4) which supports the idea that older subjects rely more on high-level information to discriminate the walking direction of point-light walkers.

A comparison of Figs. 3 and 4, suggests that the inversion effect for stimuli without noise is bigger for a stimulus duration of 40 frames in Experiment 1 than in Experiment 2. This accuracy difference may have two explanations. First, Fig. 3 shows response accuracy for only 10 practice trials in which subjects saw inverted point-light walkers for the first time, whereas Fig. 4 shows response accuracy for inverted walkers presented after an initial practice phase. It has to be noted, as well, that subjects in Fig. 4 had been exposed to a lot more trials of various different stimulus durations. Therefore, differences in learning, or the familiarity of inverted point-light walkers, might have contributed to the different levels of performance obtained with inverted walkers in Experiments 1 and 2. Second, between-subject variability was much greater in older subjects than younger subjects.

It has been suggested that neurophysiological changes in lower level visual areas are responsible for the decline in processing low-level visual motion stimuli (Blake et al., 2008; Bennett et al., 2007). For example, lower level visual areas such as V1 and MT show increased levels of noise and decreased levels of inhibitory neurotransmitters in senescent monkeys and cats (Hua, Kao, Sun, Li, & Zhou, 2008; Leventhal et al., 2003; Liang et al., 2008; Schmolesky et al., 2000; Yang et al., 2008, 2009; Yu et al., 2006). Those functional changes might be responsible for older subjects' decreased ability to perceive and process low-level motion stimuli. However, higher-level dynamic stimuli such as point-light walkers also engage areas that are not necessarily involved in the processing of lower-level visual motion stimuli, such as the superior temporal sulcus (Grossman & Blake, 2001, 2002; Grossman, Blake, & Kim, 2004). Therefore, one reason for older subjects' ability to process high-level visual motion stimuli as efficiently as younger subjects might be that higher-level visual areas like STS are less affected by age-related changes.

A recent theory described by Giese and Poggio (2003) is relevant here: Giese and Poggio (2003) proposed that the dorsal motion pathway processes biological motion by analyzing optic-flow patterns, whereas the ventral pathway processes biological motion by analyzing sequences of "snapshots" of body shapes. Information from both pathways might be integrated into a single percept, perhaps in area STS. Their hypothesis is supported by a variety of psychophysical and brain imaging studies in normal young adults (e.g., Grossman & Blake, 2002; Cutting, Moore, & Morrison, 1988), and by studies showing that patients with lesions in the dorsal pathway are able to process biological motion stimuli (McLeod, Dittrich, Driver, Perrett, & Zihl, 1996; Vaina, Lemay, Bienfang, Choi, & Nakayama, 1990). The Giese and Poggio framework also may provide an explanation for the small age difference found with walkers presented without noise: Specifically, older subjects might be able to compensate for loss or changes in lower-level motion processing by relying primarily on ventral areas when processing higher-level motion stimuli. In other words, older subjects may compensate for changes in low-level mechanisms by using information conveyed by different neural networks. This hypothesis is consistent with previous neuroimaging studies showing that, for example, the neural systems correlated with spatial frequency discrimination differ for younger versus older subjects (Bennett, Sekuler, McIntosh, & Della-Maggiore, 2001). Therefore, it is plausible to suggest that processing of higher-level visual stimuli, such as point-light walkers, may engage different neural networks in older and younger subjects. In the case of lower-level visual motion stimuli, such as apparent motion and/or random dot kinematograms, which do not necessarily allow higher-level cognitive interpretations, older adults might have to solely rely on the processing capacities of lower-level visual areas and hence, show larger processing deficits for those kinds of stimuli.

Results from Experiment 2 support the hypothesis that global form information is sufficient for both age groups to discriminate the walking direction of point-light walkers. Both age groups performed equally well for random-position walkers. Nevertheless, even in the absence of noise, an age difference for normal walkers was still preserved at certain stimulus conditions. Random-position walkers primarily contain information about the global form of the walker whereas normal walkers contain both local motion and global form information.

Therefore, the age difference for processing normal walkers might indicate age-related difficulties integrating form and motion information into a single percept. It seems as if older subjects need more time to process normal walkers, because the age-difference is most prominent for short stimulus durations. In addition, older subjects also exhibited an increased inversion effect. Previous studies have suggested that inversion disrupts the processing of the global form of the walker (Pavlova & Sokolov, 2000; Sumi, 1984; Troje & Westhoff, 2006). The increased inversion effect for older subjects in the current experiments is an interesting phenomenon that has not been observed previously. In face recognition it has been shown that older and younger subjects exhibit similar inversion effects (Boutet & Faubert, 2006). Therefore, it seems especially intriguing that older subjects exhibit such a tremendously increased inversion effect for point-light walkers. As stated above, one reason might be that older subjects are less able to use the motion information available in the stimulus and are less able to integrate the motion and form information into a single percept. But in addition to a difference in processing global form and local motion information, also the level of experience might play a role. A hypothesis that has been put forward in the context of face inversion is that inversion effects are not necessarily due to qualitative processing differences between upright and inverted stimuli but rather due to the processing efficiency based on the experience we have with a certain stimulus (Sekuler et al., 2004; Gaspar, Bennett, et al., 2008; Gaspar, Sekuler, et al., 2008). Because we are less experienced with inverted stimuli, we might simply be less able to use the information that is available to us in inverted stimuli. Recent studies have shown that inversion effects can, in fact, increase with experience (Husk, Bennett, & Sekuler, 2007; Hussain, Sekuler, & Bennett, 2009). So it is reasonable to expect that such experience-dependent effects might increase with age. In this context, older subjects might simply be less efficient at extracting relevant information for direction discrimination from inverted walkers, because less high-level information is available to compensate the loss in the lower-level visual areas for motion processing.

Taken together, the results from the two experiments presented in the current paper suggest that older subjects have difficulties extracting relevant information from noisy displays. These results might have important implications for older subjects' every day lives also in more behaviourally relevant situations when searching for objects or people in cluttered environments, for example when searching for a certain product in the supermarket or finding a friend in a crowd of people. In addition, although both older and younger subjects seem to rely more on the global form than local motion information when discriminating point-light walkers, this effect seems to be more pronounced in older subjects. Older subjects seem to have difficulties integrating local motion and global form information as efficiently as younger subjects, which might be due to a deficiency in processing low-level motion in which case higher-level visual mechanisms seem to be able to compensate, at least partially, for loss in primary visual functions. Future research needs to investigate and identify those mechanisms in further detail.

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