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Social attention is crucial for efficient social interactions and adaptive functioning in humans. However, whether this indispensable ability is unique and qualitatively distinct from nonsocial attention remains equivocal. Using the visual adaptation technique in conjunction with a modified central cueing paradigm, the current study investigated the specificity of social attention. Results revealed that adaptation to the walking direction of biological motion (BM) affected the reflexive attentional effect triggered by subsequent BM cues. Critically, preexposure to another type of social cues (i.e., eye gaze) could produce a similar aftereffect on attentional orienting elicited by BM, reflecting that social attention induced by different types of cues might share common neural substrates. By contrast, such cross-category adaptation aftereffect disappeared when adaptors changed to nonsocial cues (i.e., arrows). In the same vein, adaptation to BM cues could also exert an aftereffect on gaze cueing but not arrow cueing effect. Taken together, these findings provide evidence for the view that "social attention is special" and support the existence of "social attention detector" in the human brain.

Keywords: social attention, biological motion, eye gaze, visual adaptation

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Sharing attention with interactive social partners, known as *social attention*, is an indispensable human ability that plays a vital part in everyday social interaction and nonverbal communication (Birmingham & Kingstone, 2009; Frischen, Bayliss, & Tipper, 2007). This fundamental ability enables people to detect what others are focusing on and to further infer their mental states (e.g., interests, emotions, intentions) and predict future behaviors (Nummenmaa & Calder, 2009). Such ability develops early in life (Farroni, Massaccesi, Pividori, & Johnson, 2004; Hood, Willen, & Driver, 1998) and appears to underpin the development of complex sociocognitive skills (e.g., theory of mind, language; Baron-

Cohen, 1995b; Brooks & Meltzoff, 2005; Shepherd, 2010). A modified central cueing paradigm, introduced by Friesen and Kingstone (1998), has been widely used to explore the properties of social attention. During the task, a nonpredictive social cue (e.g., eye gaze) is presented at the center of the screen, followed by a peripheral target (a Gabor patch or a letter) appearing either on the same side indicated by the social cue (congruent) or on the opposite side (incongruent). Although participants are clearly informed that the cue is uninformative of the target location, the social cue is potent enough to drive participants to shift their attention to the cued location, resulting in a facilitated response time (RT) in the congruent condition than the incongruent condition. This effect occurs very fast (as early as 100 ms; Friesen & Kingstone, 2003; Langton & Bruce, 1999) and even when the cue direction is counterpredictive of target location (Driver et al., 1999; Friesen, Ristic, & Kingstone, 2004). As such, this orienting of attention exerted by social cues has typically been viewed as automatic and reflexive (Driver et al., 1999; Friesen & Kingstone, 1998; Friesen et al., 2004; Frischen et al., 2007; Langton & Bruce, 1999).

The eyes, as the "window to the soul," provide the most reliable and salient cue to other's direction of attention (Baron-Cohen, 1995b; Emery, 2000). There is a bounteous source of studies concerning the particular function of eye gaze in social attention. Intriguingly, reflexive attentional orienting effect induced by gaze can also be observed in nonhuman primates (e.g., monkeys), suggesting an evolutionary basis for the mechanism of such attentional effect (Deaner & Platt, 2003). The preservation of this ability across species raises the possibility that gaze-mediated attentional orienting might conceivably involve some specialized mechanisms devoted exclusively to computing where eye gaze is directed (i.e., eye-direction detector), as implied by Baron-Cohen (1995a). Albeit exhibiting different perceptual properties com-

pared to the eye gaze cues, the walking direction of biological motion (BM) cues portrayed by a handful of moving point-light dots attached to the main joints of a person (Johansson, 1973) has also been found to trigger the reflexive attentional effect (Shi, Weng, He, & Jiang, 2010). Moreover, this effect emerges in preschool children and 6-month-old infants (Bardi, Di Giorgio, Lunghi, Troje, & Simion, 2015; Zhao et al., 2015). In particular, such BM-induced attentional orienting effect can occur in the absence of any global configuration and without observers' subjective awareness of its biological nature (Wang, Yang, Shi, & Jiang, 2014). In light of all the aforementioned findings, it is reasonable to hypothesize that there might exist a functionally specific brain mechanism tailored to identify the direction of the limbs of another creature in locomotion (i.e., life motion detector), which may act in an analogous manner as the eye-direction detector (Troje & Westhoff, 2006; Wang et al., 2014; Wang et al., 2020). However, the existence of such dedicated detector module is not yet proved empirically. Further, this conjecture raises an important question as to whether the reflexive attentional orienting effects produced by BM stimuli and eye gaze share common underlying neural mechanisms that are tuned to social attention.

On the other hand, the original idea that "social attention is special" has been challenged by many studies which found automatic attentional effect evoked by nonpredictive symbolic directional cues (e.g., arrows; Hommel, Pratt, Colzato, & Godijn, 2001; Ristic, Friesen, & Kingstone, 2002; Ristic & Kingstone, 2006; Tipples, 2002). Attempts to investigate the uniqueness of social attention by directly comparing eye gaze and arrow cues in a cueing task have yielded mixed results. Some researchers have demonstrated that eye gaze can trigger more strongly reflexive shift of attention than arrows, as the former is less susceptible to top-down cognitive control (e.g., the manipulations of cue predictability or cue-target color congruency; Friesen et al., 2004; Ristic, Wright, & Kingstone, 2007), whereas others raised disagreement that nonsocial cues could trigger a comparable and indistinguishable reflexive attentional effect to social cues (Nummenmaa & Hietanen, 2009; Tipples, 2008). In addition, neuropsychological and neuroimaging studies trying to shed light on the neural systems involved in social and nonsocial attention have also produced inconsistent results. For instance, there is evidence from studies with brain-damaged and schizophrenia patients that the superior temporal gyrus (STG; Akiyama et al., 2008; Akiyama et al., 2006) and the amygdala (Akiyama et al., 2007) are specialized for attentional effect evoked by eye gaze. Moreover, some fMRI (Hietanen, Nummenmaa, Nyman, Parkkola, & Hämäläinen, 2006; Joseph, Fricker, & Keehn, 2015) and ERP studies (Hietanen, Leppänen, Nummenmaa, & Astikainen, 2008) have demonstrated that gaze and arrow cueing engage different attention systems— the former tends to activate the ventral attentional network (involved in bottom-up process) whereas the latter appears to recruit the dorsal attentional network (involved in top-down process; but see Engell et al., 2010). However, opposite evidence has also been found in other brain imaging studies showing that gaze- and arrow-triggered orienting exhibits a very similar pattern of brain activation (Sato, Kochiyama, Uono, & Yoshikawa, 2009; Tipper, Handy, Giesbrecht, & Kingstone, 2008; Uono, Sato, & Kochiyama, 2014). Taken together, existing findings are rather equivocal with regard to the questions whether social attention is fundamentally distinct from nonsocial attention and relies on spe-cialized neural mechanisms shared by different types of social cues (e.g., eye gaze and BM stimuli).

To directly probe these issues, the current study investigated the specialized mechanisms underlying social attention using a combination of the visual adaptation technique and a modified central cueing paradigm. Visual adaptation refers to the process that prolonged exposure to a visual stimulus results in a temporal suppression of the neurons selectively tuned to the adapted feature and hence influences subsequent perception (Köhler & Wallach, 1944). Adaptation is a central characteristic of almost all neural systems and can be measured behaviorally in the form of perceptual aftereffects. Therefore, visual adaptation technique, termed as "the psychologist's microelectrode" (Frisby, 1980), offers a non-invasive and powerful tool for exploring the existence of a specific neural module underlying the adapted feature, from low-level stimulus features (e.g., motion, orientation; Clifford, 2002) to high-level object properties (e.g., facial identity, gaze direction; Jenkins, Beaver, & Calder, 2006; Leopold, O'Toole, Vetter, & Blanz, 2001). Here, we used this technique to examine whether there exists a neural module dedicated to the attentional effect triggered by BM cues. Aside from the same-category adaptation (BM-to-BM), we also used the cross-category adaptation (gaze-to-BM) to test whether the specialized neural module underlying BM-triggered orienting can be shared across a different type of social cues (i.e., eye gaze). In addition, nonsocial adaptors (arrows) were used (arrow-to-BM) to investigate whether the cross-category adaptation aftereffect, if observed, is specific to social attention module. In the same vein, BM cues were also used as adaptors in the cross-category adaptation paradigm (BM-to-arrow and BM-to-gaze) to further seek a double dissociation between social and nonsocial attention.

Method

Participants

A total of 160 college students whose ages ranged from 18 to 27 ($M \pm SD = 22.2 \pm 2.1$) years took part in the study, with 32 participants (18 women in Experiments 1 and 2, 16 women in Experiment 3, 21 women in Experiment 4, and 19 women in Experiment 5) in each of the five experiments. All participants had normal or corrected-to-normal vision and were naïve to the purpose of the experiments. They all gave written informed consent in accordance with procedure and protocols approved by the institutional review board of the Institute of Psychology, Chinese Academy of Sciences. A two-tailed power analysis using G*Power (Version 3.1.9.4; Faul, Erdfelder, Lang, & Buchner, 2007) indicated that a sample size of at least 24 participants would afford 80% power to detect a medium-high attentional effect (Cohen's $d = 0.60$) induced by BM cues, which was found in a previous study with an identical design (Shi et al., 2010). We have further increased the sample size to 32 per experiment to adequately detect the potential interactions in the current study.

Stimuli

Stimuli were displayed using MATLAB (Mathworks, Inc., Natick, MA) together with the Psychtoolbox extensions (Brainard, 1997; Pelli, 1997) on a 19-in. CRT monitor (1,280 × 1,024 at 60

Hz). BM stimuli for all experiments, which were created by capturing the motion of a walking actor, were adopted from Vanrie and Verfaillie (2004). Each BM sequence (subtended approximately $3.6° \times 6.1°$ in visual angle) consisted of 13 white point-light dots depicting the motions of the head and the major joints (shoulders, elbows, wrists, hips, knees and ankles). Each cycle was 1 s and contained 30 frames. The initial frame of the point-light display was randomized for each trial to avoid observers' prediction. In Experiment 1, point-light BM stimuli with leftward or rightward walking direction were employed as the adapting stimuli. In Experiment 2, the adaptors were black and white neutral face images ($4.3° \times 5.3°$) with gaze averted to the left or right. The face images were taken from the Ekman and Friesen's Pictures of Facial Affect (Ekman & Friesen, 1976), and they were cropped to remove features outside of the face (e.g., hair and ears). The gaze direction was manipulated by using Photoshop software. In Experiment 3, white arrows pointing leftward or rightward ($1.7° \times 1.4°$) were used as the adapting stimuli. Arrows were created by combining a straight line and an arrowhead attached to the leading end of the line. These arrows were used as central cues in Experiment 4. The same face images from Experiment 2 were adopted in Experiment 5 as the central cues. All stimuli were presented on a gray background (RGB: 128, 128, 128), and the viewing distance was about 57 cm.

Procedure

Experiment 1. Experiment 1 consisted of two phases: a baseline phase and an adaptation phase which comprised two blocks (adaptation to the left direction and adaptation to the right direction). A modified central cueing paradigm was adopted in the baseline phase. Each baseline trial began with fixation on a central cross ($0.7° \times 0.7°$) within a white frame ($17.9° \times 17.9°$). After 1000 ms, a BM cue either walking toward left or right appeared in the center of the screen for 500 ms. After an interstimulus interval (ISI) of 100 ms, a Gabor patch ($1.2° \times 1.2°$) was briefly presented for 100 ms as a target on the left or right side of the screen at a distance of $4.5°$ from the central cross. Participants were required to press one of two arrow keys to indicate the location of the target (left arrow key for left target and vice versa) as quickly as possible but had to give priority to response accuracy. Participants were asked to fixate on the central cross throughout the trial. The baseline phase contained 80 trials with 40 congruent trials (the target location and the walking direction were the same) and 40 incongruent trials (the target location and the walking direction were opposite to each other), and there was a short rest break after 40 trials. At the beginning of the task, participants were explicitly told that the walking direction of BM stimuli did not predict target location. The trials were presented in a randomized order for each observer.

The adaptation phase (see Figure 1A) started with a 25-s preadaptation, during which a point-light walker walking toward a certain direction (left or right) was presented. To avoid local adaptation during this adaptation period, the center of the BM stimulus floated randomly within an area of $1.8° \times 1.8°$. The color of the point-light walker changed to red every few seconds (3–5 s) and participants were required to follow the movement of the stimulus and press the space key immediately when they detected the color change. This color detection test was administered to ensure attention throughout the adaptation period. Performance of the color detection task was high (97.0%), showing that these participants indeed paid attention to the adapting stimuli. The preadaptation period was immediately followed by a test period of 80 trials which was exactly the same as in the baseline phase. Participants were asked to fixate on the fixation and respond to the location of the target following a central BM cue. After every four trials, there was a 5-s additional topping-up adaptation without color change to maintain the adaptation effect. The sequence of the two adaptation blocks (adaptation to left or right direction) was counterbalanced between participants. Half of the participants adapted to point-light BM stimuli walking leftward in the first block and then adapted to right direction in the second block. And the order was reversed for the other half participants.

Prior to each phase, participants were given practice trials until their correct response rates for target localization task were over 90%. In addition, they had to reach 80% accuracy in the color detection task in the adaptation phase.

Experiment 2. Experiment 2 followed the same design and procedure as in Experiment 1, except that both the preadapting stimulus and the topping-up stimulus were changed to face images with averted eye gaze in the adaptation phase. Accordingly, the irises of the eyes turned red occasionally which required a quick response (see Figure 1B). In this experiment, color detection performance was also close to perfection (96.2%), again reflecting that participants were able to attend to the adaptors.

Experiment 3. Experiment 3 was identical in structure to Experiment 1, with the only difference being that arrows pointing leftward or rightward instead of BM stimuli were used as the adapting stimuli. The participants were required to press the space key when they detected a color change from white to red (see Figure 1C). Performance on this task was again very high (96.6%).

Experiment 4. In contrast to Experiment 3, arrows and BM stimuli switched their roles in Experiment 4, namely arrows were used as central cues and BM stimuli as adaptors. The procedure of the arrow cueing task employed in the baseline phase and the test period was similar to that of the BM cueing task with the exception that arrows were presented for 300 ms rather than 500 ms. Similarly, a 5-s topping-up adaptation was embedded after every two test trials to obtain stronger adaptation effect. There was also a blank interval jittered between 700 and 1,200 ms after the BM adaptor disappeared. In addition, participants performed the BM color detection task in the preadaptation period with very high accuracy (97.2%).

Experiment 5. The procedure was identical to that of Experiment 4 except that arrow cues were replaced by gaze cues. Participants again showed high accuracy on the BM color detection task (96.0%).

Results

For all five experiments, trials with incorrect responses and RTs shorter than 100 ms or longer than 1,800 ms were excluded from the statistical analyses, followed by trials with RTs beyond three standard deviations above or below the mean (collapsed across experimental conditions). The percentage of trials excluded from the analyses was 2.7% in Experiment 1, 2.7% in Experiment 2, 2.0% in Experiment 3, 3.0% in Experiment 4, and 2.6% in Experiment 5.
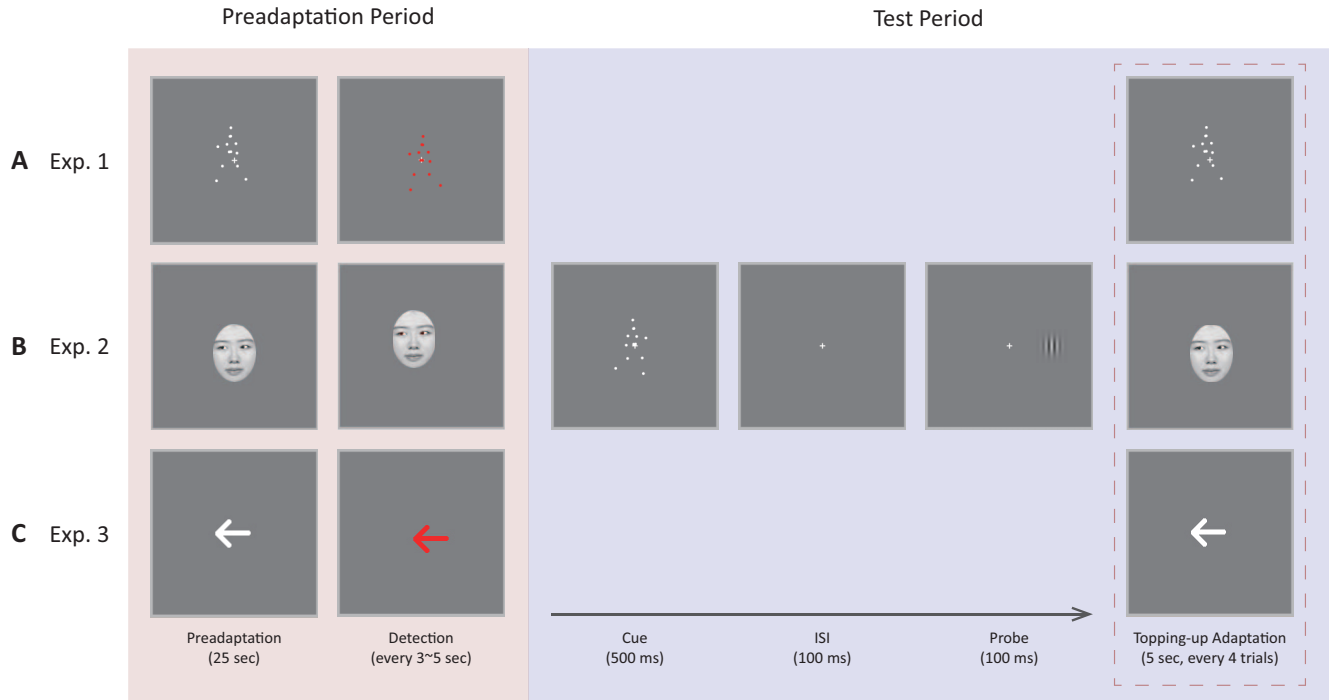
Figure 1. Schematic representation of the adaptation phase in Experiments 1–3. A: The adaptation phase in Experiment 1 started with a 25-s preadaptation period, during which a biological motion (BM) stimulus with leftward or rightward walking direction was presented. Participants were required to follow the movement of the stimulus and detect the color change. The preadaptation period was immediately followed by a test period that adopted a modified central cueing paradigm (exactly the same as in the baseline phase). During the test period, participants were required to indicate the location of a target following a brief presentation of a central BM cue in each trial. In addition, there was a 5-s topping-up adaptation after every four trials to maintain the adaptation effect. B, C: Experiments 2 and 3 followed the same design and procedure as that in Experiment 1 with the exception that both the preadapting and topping-up stimuli were changed to face images with averted eye gaze (B) or arrows (C) pointing leftward or rightward, respectively. The face image of Haoyue Ji is shown in Figure 1B for illustration purpose. See the online article for the color version of this figure.

Experiment 1

In the baseline phase of Experiment 1, a paired-*t* test showed that participants responded faster to targets presented at the same location (congruent condition) indicated by the walking direction of BM stimuli than to those presented at the opposite location (incongruent condition; 343 ms vs. 348 ms, $t(31) = -2.34$, $p = .026$, $d = 0.41$, 95% confidence interval (CI) for the mean difference $[-9, -1]$), even they were explicitly told that the BM cues didn't predict the target location. This result suggests that reflexive attentional effect can be observed with the walking direction of BM, which is in line with previous studies (Shi et al., 2010; Wang et al., 2014; Zhao et al., 2015). In the adaptation phase, a 2 (adaptation condition: adapted vs. unadapted) × 2 (congruency: congruent vs. incongruent) repeated measures analysis of variance (ANOVA) of mean RTs revealed a main effect of adaptation condition, $F(1, 31) = 10.54$, $p = .003$, $\eta_p^2 = 0.25$, but not congruency, $F(1, 31) = 3.06$, $p = .090$, $\eta_p^2 = 0.09$. Crucially, the interaction between adaptation condition and congruency was significant, $F(1, 31) = 5.85$, $p = .022$, $\eta_p^2 = 0.16$, 95% CI for the interaction effect $[5, 12]$. Further analyses revealed that the attentional effect observed in the baseline phase disappeared when the

walking direction of BM was in the same direction as the preceding adaptor (adapted condition; 368 ms vs. 368 ms, $t(31) = 0.02$, $p = .983$, $d = 0.00$, 95% CI for the mean difference $[-6, 6]$) but preserved when the BM cues were opposite to the adapted direction (unadapted condition; 359 ms vs. 367 ms, $t(31) = -2.81$, $p = .008$, $d = 0.50$, 95% CI for the mean difference $[-14, -2]$; see Figure 2A, and Supplementary Figure S1A in the online supplemental material for the panorama of the data). Note that the effect size was reduced to zero in the adapted condition but was in the normal magnitude in the unadapted condition. The distinction between these two conditions was further highlighted by the magnitude of the attentional effect calculated using the difference in the mean RT obtained under the incongruent condition versus that under the congruent condition divided by their sum ($RT_{incongruent} - RT_{congruent}/RT_{incongruent} + RT_{congruent}$). The normalized effect decreased greatly in the adapted condition compared to that in the unadapted condition (0 vs. 0.011, $t(31) = -2.45$, $p = .020$, $d = 0.43$, 95% CI for the mean difference $[-21, 0]$). We also used the mixed effects modeling approach to reexamine the generalizability of our main findings and found basically equal results (see the online supplemental materials). Collectively, these results
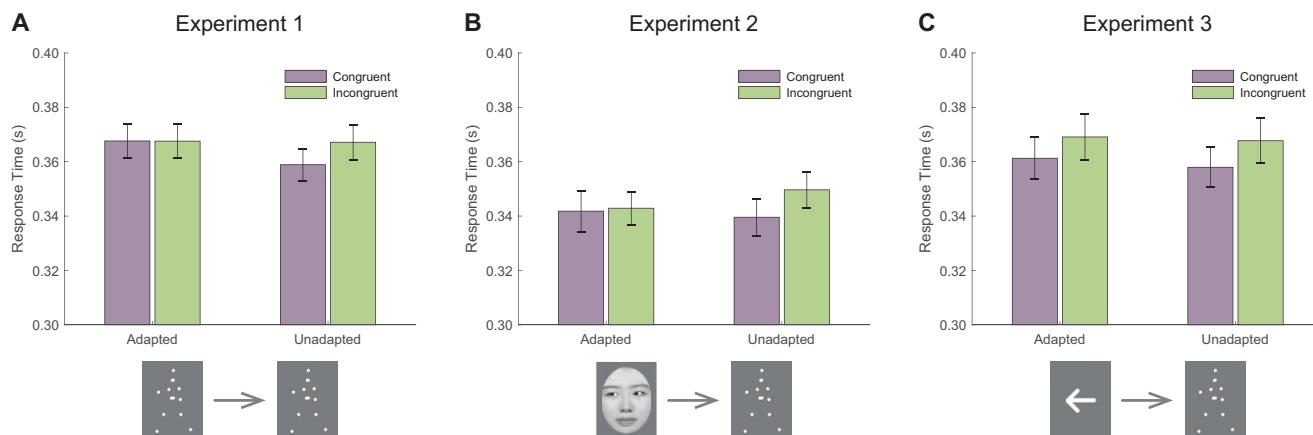
Figure 2. Results from Experiments 1–3. A: In Experiment 1 (BM-BM adaptation), the attentional effect disappeared when the walking direction of BM was in the same direction as the preceding adaptor (adapted condition) but preserved when the BM cues were opposite to the adapted direction (unadapted condition). B, C: Such adaptation aftereffect was also observed in Experiment 2 (gaze-BM adaptation, B) but vanished in Experiment 3 (arrow-BM adaptation, C). Error bars show standard errors. BM = biological motion. The face image of Haoyue Ji is shown in Figure 2B for illustration purpose. See the online article for the color version of this figure.

clearly demonstrated an effect of adaptation on social attention elicited by the walking direction of BM.

Experiment 2

In Experiment 2, we further investigated whether the adaptation aftereffect of social attention obtained in Experiment 1 could also be found when another type of social cues (i.e., eye gaze) served as the adapting stimuli. Again, a significant reflexive attentional orienting effect induced by BM cues was observed in the baseline phase, replicating Experiment 1 (343 ms vs. 348 ms, $t(31) = -2.25$, $p = .032$, $d = 0.40$, 95% CI for the mean difference [−10, 0]). In the adaptation phase, results revealed a significant main effect of congruency, $F(1, 31) = 4.52$, $p = .042$, $\eta_p^2 = 0.13$ but no main effect of adaptation condition, $F(1, 31) = 2.89$, $p = .099$, $\eta_p^2 = 0.09$. Similar to Experiment 1, a significant interaction between adaptation condition and congruency was found ($F(1, 31) = 4.73$, $p = .037$, $\eta_p^2 = 0.13$, 95% CI for the interaction effect [5, 13]). Furthermore, we found that adaptation to the gaze direction could affect the attentional effect triggered by BM cues, as revealed by the vanished attentional effect of BM cues in the adapted condition (342 ms vs. 343 ms, $t(31) = -0.29$, $p = .777$, $d = 0.05$, 95% CI for the mean difference [−9, 7]) but the normal level of attentional effect in the unadapted condition (340 ms vs. 350 ms, $t(31) = -3.53$, $p = .001$, $d = 0.62$, 95% CI for the mean difference [−16, −4]; see Figure 2B and Supplementary Figure S1B in the online supplemental material). Again, the normalized attentional effect was significantly smaller in the adapted condition than that in the unadapted condition (0.003 vs. 0.015, $t(31) = -2.14$, $p = .040$, $d = 0.38$, 95% CI for the mean difference [−24, −1]). Overall, these findings together demonstrated that adaptation to social attention could be effective across different types of social cues (eye gaze and walking direction of BM), thereby providing evidence for common neural substrates

underlying social attention induced by eye gaze and walking direction of BM.

Experiment 3

To ensure that the cross-category adaptation aftereffect observed in Experiment 2 was unique to social attention, we adopted nonsocial cues (i.e., arrows) as adapting stimuli in Experiment 3. As expected, we found a significant reflexive attentional effect in the baseline phase (360 ms vs. 364 ms, $t(31) = -2.11$, $p = .043$, $d = 0.37$, 95% CI for the mean difference [−9, 0]), which paralleled the findings obtained in Experiment 1 and Experiment 2. In the adaptation phase, no significant main effect of adaptation condition was found, $F(1, 31) = 2.74$, $p = .108$, $\eta_p^2 = 0.08$. Importantly, there was a significant main effect of congruency, $F(1, 31) = 10.60$, $p = .003$, $\eta_p^2 = 0.26$, whereas the interaction between adaptation condition and congruency was not significant ($F(1, 31) = 0.44$, $p = .514$, $\eta_p^2 = 0.01$, 95% CI for the interaction effect [−1, 5]), thus reflecting that BM cues could produce significant reflexive attentional orienting effects in both adaptation conditions (adapted and unadapted), and the attentional effects did not differ with each other (see Figure 2C and Supplementary Figure S1C in the online supplemental material). In a nutshell, the exposure to nonsocial cues failed to cause adaptation aftereffect.

Experiment 4

To investigate if there exists a double dissociation between social and nonsocial attention, we tested the conversed effect, that is, whether BM adaptation could modulate arrow cueing. Similar to Experiment 3, results showed that nonpredictive arrow cues could trigger similar orienting effect in the adaptation phase (congruency: $F(1, 31) = 7.61$, $p = .010$, $\eta_p^2 = 0.20$) as in the baseline phase (362 ms vs. 378 ms, $t(31) = -4.67$, $p < .001$, $d = 0.83$,

95% CI for the mean difference [−22, −9]), without a noticeable difference between the adapted and the unadapted condition (interaction: $F(1, 31) = 0.41$, $p = .527$, $\eta_p^2 = 0.01$, 95% CI for the interaction effect [−7, 1]; see Figure 3A and Supplementary Figure S1D in the online supplemental material). Again, no main effect of adaptation condition was observed, $F(1, 31) = 0.15$, $p = .706$, $\eta_p^2 = 0.01$. In sum, these converging findings of Experiment 4 and Experiment 3 confirmed a double dissociation between social and nonsocial attention and supported the hypothesis that there might exist a specialized neural network subserving social but not nonsocial attention.
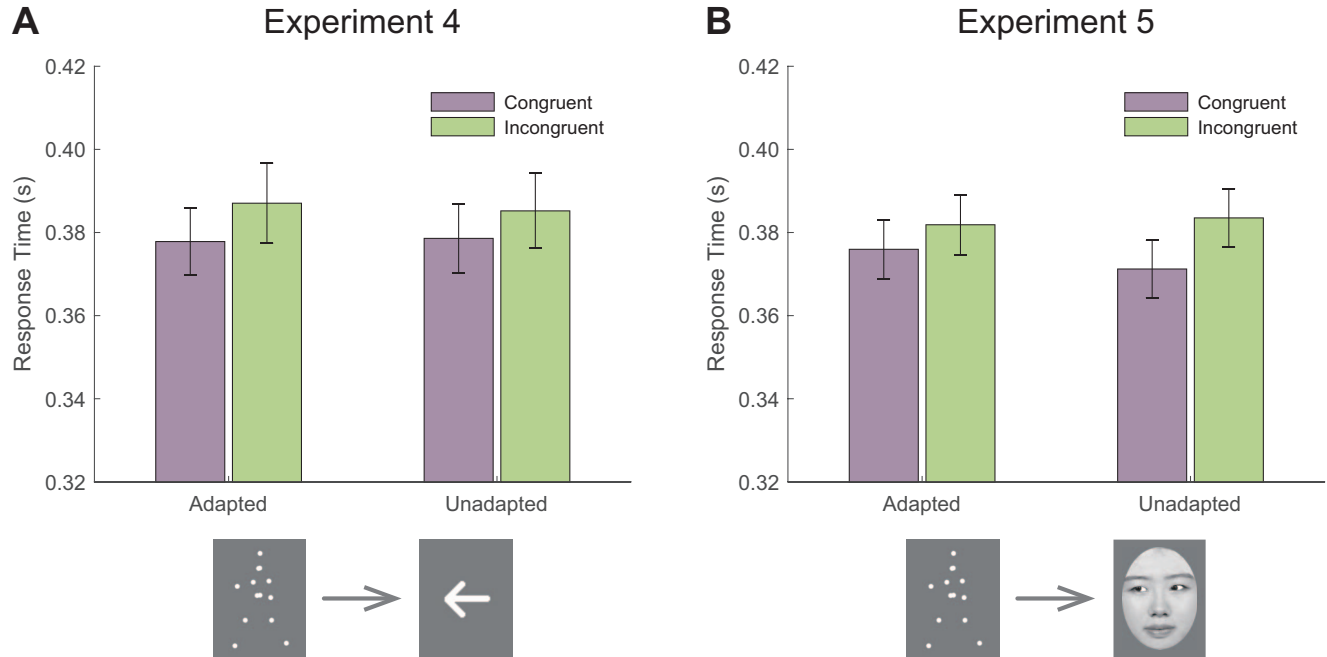
Experiment 5

In Experiment 5, we further explored whether BM adaptation, which failed to affect arrow cueing, could exert influences on gaze cueing. In the baseline phase, we found an attentional orienting effect triggered by nonpredictive eye gaze cues that was repeatedly confirmed by previous studies (Driver et al., 1999; Friesen & Kingstone, 1998; 368 ms vs. 376 ms, $t(31) = −3.32$, $p = .002$, $d = 0.59$, 95% CI for the mean difference [−13, −3]). After adapting to BM walkers, a 2×2 ANOVA showed a significant main effect of congruency, $F(1, 31) = 23.13$, $p < .001$, $\eta_p^2 = 0.43$ but no main effect of adaptation condition, $F(1, 31) = 1.95$, $p = .172$, $\eta_p^2 = 0.06$. In contrast to Experiment 4, there was a significant interaction between adaptation condition and congruency which dovetailed with Experiment 2 ($F(1, 31) = 4.77$, $p = .037$,

$\eta_p^2 = 0.13$, 95% CI for the interaction effect [4, 9]; see Figure 3B and Supplementary Figure S1E in the online supplemental material). Subsequent analyses revealed that the normalized reflexive attentional effect was significantly weakened in the adapted condition as opposed to the unadapted condition (0.008 vs. 0.016, $t(31) = −2.20$, $p = .036$, $d = 0.39$, 95% CI for the mean difference [−17, −1]). In conclusion, these findings together with Experiments 2–4 converged upon the view that the adaptation aftereffects of social attention exhibited a cross-category property within the social but not nonsocial domain, thereby providing evidence for a specialized "social attention detector" in the human brain.

Discussion

Humans are endowed with a remarkable ability to coordinate attention between others in reference to an event or object in the environment (Nummenmaa & Calder, 2009). In the current study, we implemented the visual adaptation technique combined with a modified central cueing paradigm to elucidate the specificity of this social attention behavior. We found that preexposure to point-light BM sequences produced an adaptation aftereffect to social attention elicited by BM cues. More specifically, the reflexive orienting of attention induced by BM cues is only observed when the cue direction is incongruent with the direction of the prior adaptors, while such orienting effect is ruined by the adaptors with the same direction as the cue. Importantly, prolonged viewing of

Figure 3. Results from Experiments 4 and 5. A: In Experiment 4 (BM-arrow adaptation), arrow cueing was not affected by preexposure to BM adaptation since no significant difference was found between the adapted and the unadapted condition. B: A cross-category adaptation between eye gaze and the walking direction of BM was found in Experiment 5 (BM-gaze adaptation). The gaze cueing effect was reduced in the adapted condition compared with that in the unadapted condition. Error bars show standard errors. BM = biological motion. The face image of Haoyue Ji is shown in Figure 3B for illustration purpose. See the online article for the color version of this figure.

another distinctively different social cue (i.e., eye gaze) can also modulate BM-mediated attentional orienting and vice versa, reflecting a remarkable cross-category adaptation aftereffect between eye gaze and the walking direction of BM. These findings together provide robust and unambiguous evidence that common neural substrates might be involved in triggering these two different types of social attention behaviors. Moreover, the lack of cross-category adaptation aftereffect between social (i.e., BM) and nonsocial cues (i.e., arrows) further suggests that the neural mechanism underlying social attention is unique and substantially distinct from that subserves nonsocial attention.

Recent studies have demonstrated that shifting attention to where point-light BM walkers are moving toward is reflexive (Shi et al., 2010; Wang et al., 2014) and emerges early in life (Bardi et al., 2015; Zhao et al., 2015), indicating that it may be an intrinsic behavior supported by a specialized neural module (i.e., life motion detector; Troje & Westhoff, 2006). The strong adaptation effect of BM-induced orienting observed in the current study offers initial evidence for the existence of such detector in the visual system tuned to social attention triggered by BM cues. Moreover, this finding critically replenishes the current mainstream literature with respect to the reflexive attentional orienting triggered by the mostly investigated social stimuli (i.e., eye gaze; Driver et al., 1999; Friesen & Kingstone, 1998; Ji, Wang, & Jiang, 2017; Sato, Kochiyama, Uono, & Toichi, 2016; Sun, Yu, Zhou, & Shen, 2017) and brings into the question whether the reflexive social attention of BM cues and eye gaze are driven by common underlying neural mechanisms. Some researchers have proposed a general "direction of attention detector" for processing all kinds of potential social attention cues (e.g., eyes, head or body) to compute the whereabouts of others' focus of interest (Perret & Emery, 1994). Along with this view, several neuroimaging and neuropsychological studies have demonstrated that the superior temporal sulcus (STS) region, which is shown to play a key part in the reflexive attentional orienting induced by eye gaze cues (Akiyama et al., 2008; Kingstone, Tipper, Ristic, & Ngan, 2004), is also involved in the processing of BM stimuli (Jackson & Blake, 2010). Here, we found novel cross-category adaptation aftereffects (gaze-to-BM and BM-to-gaze), suggesting that the reflexive social attention produced by the walking direction of BM and eye gaze recruit overlapping neural networks, thus providing compelling evidence in support of a general "social attention detector" in the human brain. Future research, combining brain imaging and visual adaptation technique, may help to identify common neural circuitry (i.e., "social attention network") subserving the reflexive orienting responses elicited by different types of social cues.

Given the fact that nonsocial cues such as arrows are found to evoke automatic attentional shifts similarly (Ristic & Kingstone, 2006; Tipples, 2002), the current study also attaches great importance to the fundamental distinction between social and nonsocial attention. Relating to this issue, existing behavioral and neuroimaging studies mostly make a direct comparison between social and nonsocial attention in a paradigm where eye gaze and arrows are presented as the central cues, yet the results are bifurcated (Engell et al., 2010; Friesen et al., 2004; Greene, Mooshagian, Kaplan, Zaidel, & Iacoboni, 2009; Joseph et al., 2015; Lockhofen, Gruppe, Ruprecht, Gallhofer, & Sammer, 2014; Marotta, Lupiáñez, Martella, & Casagrande, 2012; Nummenmaa & Hietanen, 2009; Ristic et al., 2007; Sato et al., 2009; Sato, Kochiyama, Uono, & Yo-

shikawa, 2010; Tipples, 2008; Uono et al., 2014). Several neuroimaging studies have reported that eye gaze and arrows recruit separate attention systems (Engell et al., 2010; Lockhofen et al., 2014). As an example, one fMRI study emphasizes the involvement of ventral attention network, especially the temporal parietal junction (TPJ), in the gaze-triggered but not arrow-triggered orienting (Joseph et al., 2015). However, some others found common neural substrates underlying these two types of attentional orienting (Greene et al., 2009; Sato et al., 2009; Uono et al., 2014). Because previous studies fail to reach a consensus, our study makes attempt to address this issue by using the cross-category adaptation methodology in Experiment 3 (arrow-to-BM) and Experiment 4 (BM-to-arrow). Remarkably, our results provide solid evidence to counterpose social attention to nonsocial attention by demonstrating that the adaptation of arrow cues cannot modulate the reflexive attentional effect evoked by the walking direction of BM and vice versa. That is, the involuntary allocation of attention driven by BM cues might involve a very different neural network from that driven by arrow cues. This finding, coupled with the observed cross-category, gaze-to-BM and BM-to-gaze adaptation effects, lends strong support for the distinctiveness of social attention and has implications for the existence of two dissociable (social vs. nonsocial) attention networks in the brain.

In summary, the current study demonstrates robust adaptation effects on reflexive attentional orienting triggered by BM cues when observers adapt to the same (i.e., BM cues) or different (i.e., eye gaze) social stimuli but not nonsocial stimuli (i.e., arrows). Furthermore, BM cues exert an adaptation aftereffect on gaze cueing but not arrow cueing effect. These findings together provide strong evidence that social attention might be unique and qualitatively distinct from nonsocial attention and suggest the existence of "social attention detector" in the human brain.

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