Category-specific interference of object recognition with biological motion perception

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The rapid and detailed recognition of human action from point-light displays is a remarkable ability and very robust against masking by motion signals. However, recognition of biological motion is strongly impaired when the typical point lights are replaced by pictures of complex objects. In a reaction time task and a detection in noise task, we asked subjects to decide if the walking direction is forward or backward. We found that complex objects as local elements impaired performance. When we compared different object categories, we found that human shapes as local objects gave more impairment than any other tested object category. Inverting or scrambling the human shapes restored the performance of walking perception. These results demonstrate an interference between object perception and biological motion recognition caused by shared processing capacities.

Keywords: biological motion, Navon figures, object recognition, body postures, interference

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Introduction

Humans are able to recognize biological motion under exacerbated conditions and without effort. Even if the information available is reduced to a few point lights, people can recognize a person walking (Johansson, 1973).

Whether this recognition is mediated by the motion of the point lights or by an analysis of the body form and posture is a matter of recent debate (Beintema & Lappe, 2002; Chang & Troje, 2008; Giese & Poggio, 2003; Lange & Lappe, 2006). The pattern of points in each of the stimulus frames of a point-light walker and the temporal sequence of the patterns provide information about the global form and posture of the body. This form information is sufficient to recognize a walker, to decide if it walks forward or backward, and to decide how it is oriented (Beintema, Georg, & Lappe, 2006). These results agree with the predictions of a template matching model (Lange & Lappe, 2006). The idea of using the form information for the perception of biological motion is referred to as a motion-from-form approach.

If the perception of biological motion is mediated by form, it should be processed in the same brain areas as objects and biological forms. Indeed, biological motion stimuli activate fusiform (Michels, Lappe, & Vaina, 2005; Peelen & Downing, 2005b) and occipital (Grossman & Blake, 2002; Michels et al., 2005; Peelen & Downing, 2005a; Singer & Sheinberg, 2010; Vaina, Solomon, Chowdhury, Sinha, & Belliveau, 2001; Vangeneugden, Pollick, & Vogels, 2008) form-selective areas along with the extrastriate body area (Downing, Jiang, Shuman, & Kanwisher, 2001) and the superior temporal sulcus (Bonda, Petrides, Ostry, & Evans, 1996; Grossman et al., 2000; Thompson, Clarke, Stewart, & Puce, 2005; Vaina et al., 2001; Vangeneugden et al., 2008). If biological motion and object recognition thus demand the same processing capacities, interference between both kinds of processing is expected. If the recognition of biological motion recruits form processing neural networks, a simultaneous need to process complex objects should make the task to recognize a walker more difficult.

Hunt and Halper (2008) recently showed that naive subjects had indeed difficulties in spontaneous recognition of a walker that was composed of different, complex objects instead of the usual point lights. Following this approach, we created biological motion stimuli that consisted of object images placed on the positions of the joints (Figure 1). We were specifically interested in images of human bodies, an object category that had not



Figure 1. Stimuli used in Experiment 1. (a) The dots of the classic point-light walker were replaced by objects, e.g., (b) pictures of humans, to measure the interference of form processing on biological motion recognition. The objects moved in the same way as the light points of the classical walker so that both stimuli contained the same motion information. Subjects had to decide if the stimulus walked forward or backward and were explicitly informed that the objects did not contribute information to that task. The humans walker is hyperlinked to an animated walker; click on it for a demonstration. (c–d) A number of different object categories were tested. (c) Comparison of tools, vehicles, vegetables, animals, and humans used representatives of those categories that were matched in shape. (d) Examples of the stick figures placed at the local level of an upright oriented walker. Stick figures were compared to inverted and scrambled stick figures as controls.

been tested by Hunt and Halper (2008) but that we predict should have a particularly strong interference with biological motion recognition in comparison to objects belonging to the other categories. The storage of conceptual knowledge is divided by semantic categories such as animals, plants, and artifacts (Caramazza & Mahon, 2003). Coslett, Saffran, and Schwoebel (2002) have shown that knowledge of the human body is also a distinct semantic domain. Further evidence that human figures are a special object category comes from research on the inversion effect. Like faces, and unlike many other objects, images of body postures (Reed, Stone, Bozova, & Tanaka, 2003) and biological motion stimuli (Pavlova & Sokolov, 2000; Sumi, 1984) are very difficult to recognize when presented upside down.

Experiment 1: Interference of object recognition with biological motion perception for different object categories

In Experiment 1, we intended to confirm that object recognition interferes with biological motion processing

and to test whether different object categories affect biological motion processing differently. The motionfrom-form approach would predict that biological motion perception would be most strongly impaired by object categories that involve processing of the human body.

The experiment used a classic point-light walker and ten different object walkers. These stimuli served as the basis for three different comparisons of performance.

First, we needed to show that the impairment of biological motion recognition that Hunt and Halper (2008) found in the spontaneous recognition by naive subjects can be replicated in psychophysical experiments in which subjects are fully aware that the stimuli present biological motion and that the objects are mere distractors. We compared reaction times and detection rates (see below) between the point-light walker condition and an object walker condition. In the latter one, the stimulus consisted of objects of different categories. In these experiments, subjects knew that the stimuli displayed human walking and that the objects were irrelevant to the task. This experiment therefore tested whether object recognition automatically and involuntarily interferes with biological motion perception.

Second, we compared six different walkers, each representing one object category. Categories were tools, animals, vegetables, vehicles, humans, and abstract textured shapes. The objects were matched in shape and size between categories (Figure 1c). The abstract textured shapes had the form of the tools but were filled with a random texture pattern.

In the last investigation, we explored the interference between biological motion perception and the processing of human shapes by testing walkers consisting of stick figures of the human body (Figure 1d). To manipulate the degree to which these shapes appear as human forms, we employed the body-inversion effect (Reed et al., 2003) and compared walkers composed of upright body forms with walkers composed of inverted body forms. Furthermore, we included a comparison condition in which the arrangement of the sticks was scrambled, thereby keeping all local orientation information but destroying body shape.

Methods

Subjects

All eleven stimuli were tested in a reaction time paradigm and a detection paradigm. Twelve subjects (four males) between 20 and 40 years old (average of 25.75) took part in this experiment with the reaction time paradigm. Fifteen naive subjects (five males) between 20 and 40 years old (average of 28.0) participated in the detection paradigm. None of the subjects participated in both experiments. All subjects had normal or corrected-tonormal vision and were naive to the purpose of the experiment. Before the testing started, they were informed that they had to concentrate only on the task and to ignore the local pictures, because they were irrelevant.

Setup

The biological motion stimuli presented a repeated cycle of recorded walking, with the translation subtracted (brief: "walker"). The walker was presented from a 45° sideways view in the middle of the screen, on a white background. It consisted of 12 pictures of objects. Figures 1a and 1b present examples of such walkers. Examples of the classes of objects, matched by their global form, and examples of the stick figures placed at the local level of a walker are shown in Figures 1c and 1d.

The walker could either be oriented to the left or to the right and walked forward or backward. The height and width of the walker depended somewhat on the size of the constituting elements. The maximum dimensions of the walker were 10.2×5.8 cm $(10.15^{\circ} \times 5.81^{\circ}$ viewing angle). Objects were 1.8 cm $(1.81^{\circ}$ viewing angle) in size. The start phase of the walker was randomly selected.

The subjects sat in a dimly lit room 57 cm in front of a Iiyama Vision Master 505 computer monitor (1024×768 pixel, 120 Hz). They gave manual responses with their right hand by pressing the arrow keys of the keyboard connected to the operating computer (Apple MacBook Pro, OS X 10.5.6).

Reaction time paradigm

The task was to decide as quickly as possible if the stimulus walked forward or backward. Each stimulus was shown until the subject responded, but no longer than 5 s. Thereafter, the next trial started. Stimuli were tested in blocks of 60 trials that contained one walker type, five different start phases, two walker orientations, two walking directions, and three repetitions.

Each subject began with two blocks of the classic walker condition to become familiarized with the task. Thereafter, each subject performed 12 blocks of 60 trials. The first and last blocks were again the classic walker condition. The 10 blocks in between were the object-walker conditions in randomized order. The entire experiment took between 35 and 60 min.

Detection paradigm

The task was also to decide as accurately as possible if the stimulus walked forward or backward. The stimulus was presented for one gait cycle (1.3 s). Thereafter, the screen became blank. The next trial started when the subject pressed a response key. The stimulus was embedded in a noise mask that consisted of 29, 57, 111, 218, 427, or 837 objects, which were of the same category as the walker's objects. Each object moved with the same trajectory as one of the walker joints but started from a randomly chosen location on the screen.

Each subject began with a practice session followed by two sessions of data collection. The practice session contained 480 trials of the classic walker condition, divided in four blocks. Five start phases, two walking directions, six noise levels, and two repetitions resulted in 120 trials per block. Those trials were randomized within a block. Each data collection session contained 12 blocks. The first and last block were the classic walker condition. The 10 blocks in between were the object-walker conditions in randomized order. This experiment contained a total of 3360 trials and lasted about 3.5 h for each subject, which each subject completed over several days.

Analysis

The reaction time data were analyzed by transforming reaction times (RTs) to reaction speeds (1/RT) to yield an approximately symmetric distribution. We used reaction speeds for the analysis because reaction times are not normally distributed but positively skewed; therefore, the mean does not represent the most likely reaction time and the conditions for parametric statistical tests are not fulfilled. Transforming reaction times to reaction speeds yields an approximately symmetric distribution that avoids the use of outlier rejection and allows to use the mean and associated statistical procedures since the influence of long latencies is small after the transformation (van Zandt, 2002).

Trials with reaction times under 100 ms were removed. This concerned 25 (<0.25%) of the trials. To compare reaction speeds between conditions, we calculated ANOVAs for each of the planned comparisons (classic objects, different categories, and human forms), followed if necessary by Bonferroni tests. Bonferroni post hoc tests compared each condition involved in the previous ANOVA with each other.

We included both correct and incorrect responses in the reaction speed analysis. Because the task put emphasis on speed rather than correctness, we thought that removing the incorrect responses would potentially bias the results. Moreover, subjects were very accurate in their responses (92.3% correct on average). We confirmed that a very similar pattern of results was obtained in an analysis that included only the correct trials.

To determine if speed–accuracy trade-offs were present, we calculated ANOVAs for error rates analogous to the ANOVAs for the reaction speeds for all reported experiments. No experiment gave evidence of any significant difference in error rates. Thus, speed–accuracy trade-offs were not present.

Differences between recognition rates in the planned comparisons (classic objects, different categories, human forms) were determined by ANOVAs with factors condition and number of noise dots. The factor number of noise dots, not surprisingly, always showed significant effects. Since our experimental question was focused on the comparison of walker conditions, we will only report the test results for the factor condition. Post hoc tests for the stick figures and the form-matched conditions were done with Bonferroni tests.

Results

We present the results in three parts that follow our three central questions. First, we replicate the comparison between a classic and an object walker with our paradigms. Then, we present the data of the form-matched stimuli to compare different categories. Lastly, we explore the influence of human forms on the recognition of biological motion stimuli. In each of the three parts, we show the data of both paradigms: reaction time and detection in noise.

Point lights versus objects

Reaction speeds and detection rates showed the same result (Figures 2a and 2b). It was more difficult to decide whether the walker walked forward or backward if it consisted of complex objects than if it consisted of small dots. With the reaction time paradigm (Figure 2a), the subjects were significantly faster (F(1, 11) = 33,349, P < 0.001), and with the detection-in-noise paradigm (Figure 2b), the subjects were significantly better

(F(1, 5) = 84.097, P < 0.001), in indicating the walking direction of a point-light compared to a mixed-object walker. This result confirms that object processing interferes with biological motion recognition in an automated and involuntary manner.

Different object categories

The reaction time paradigm (Figure 2c) gave a significant influence of condition (F(5, 55) = 2.693, P =(0.03). Post hoc tests showed that recognition of the walker composed of human shapes was significantly slower than those of the other five conditions (largest P < 0.001). Reaction speeds of the other comparisons did not differ significantly from each other. The detection-in-noise paradigm (Figure 2d) revealed significant differences between the compared conditions (F(5, 25) = 11,450), P < 0.001). A post hoc analysis showed that recognition performance for the human shapes and for the tools was significantly lower than that of the remaining four conditions (humans: largest P < 0.037; tools: largest P < 0.001). Recognition performance for human shapes and tools did not differ significantly from each other (Figure 2d, P = 0.843).

Specificity to the human form

The data of the stick-figure experiments (Figures 2e and 2f) showed consistent differences between the three compared conditions (reaction time: F(2, 22) = 8.540, P = 0.002; detection: F(2, 10) = 28.855, P < 0.001). Performance in both paradigms was worst for upright stick figures, better for inverted stick figures that were less recognizable as human forms, and best for the scrambled stick-figure condition, which did not resemble the human form at all. All post hoc comparisons between the three conditions showed significant differences (reaction time: largest P < 0.001; detection: largest P < 0.01). The stick figures were a more difficult condition than the scrambled or inverted stick figures.

Experiment 2: Inversion test for photos of human shapes

Experiment 1 found an inversion effect for stick figures of human bodies. The goal of Experiment 2 was to replicate this finding with photos of human bodies rather than stick figures. Moreover, Experiment 2 also included conditions in which the walker was presented upside down and the photos of human bodies were either upright or upside down (Figure 3). The experiment used the same methods and paradigms as Experiment 1.



Figure 2. Results for the different comparisons. (a, c, e) The bar charts show the results for the reaction time paradigm. Subjects had to decide as quickly as possible whether the walker walked forward or backward. The graphs show reaction speed and standard error. (b, d, f) The line graphs on the right show the results for the detection paradigm. The stimuli were embedded in noise masks of additional moving objects. Subjects had to decide as accurately as possible whether the stimulus walked forward or backward. The graphs show the proportion of correct responses (proportion correct) as a function of the number of objects in the noise mask.

Methods

In the reaction time paradigm, eleven naive subjects (four males) between 19 and 41 years old (average 27.2) participated. None had participated in Experiment 1. All subjects had normal or corrected-to-normal vision and were naive to the purpose of the experiment. Before the testing started, they were informed that they had to concentrate only on the task and to ignore the local pictures because they were irrelevant. The testing included practice and test phases. For practice, we used stimuli from Experiment 1: 120 trials of the classic condition, 60 trials of the object-walker condition, and 60 trials of the vehicle condition. The test phase consisted of 60 blocked trials for each of the four human-walker conditions. Block order was randomized between subjects.

In the detection paradigm, six (three males) subjects between 22 and 33 years old (average 27.3) participated. They had normal or corrected-to-normal vision and were naive to the purpose of the experiment. Before the session started, the subjects were informed that they had to concentrate only on the task and to ignore the local pictures because they were irrelevant. In the detection paradigm, we only included the two upright walker conditions (with upright or inverted human photos) since performance in the two inverted walker conditions were at chance level even without noise. Subjects initially practiced on 60 trials of the classic condition without noise to become familiar with the stimulus. This was followed by 120 practice trials of the classic condition and 120 practice trials of the vehicle condition. The testing phase consisted of two blocks of 120 trials for each of the two conditions, resulting in 480 trials.



Figure 3. Stimuli used in Experiment 2. The walker consisted of (a) upright or (b) inverted pictures of humans.

Results

Reaction speed in the upright photo condition of the upright walker was significantly slower than for the inverted photo condition of the upright walker (Figure 4a, F(1, 10) = 10.475, P = 0.009). The accuracy for the inverted walker was at chance level for both conditions (percent correct: 0.53 for inverted human photos and 0.55 for upright human photos), demonstrating a strong inversion effect for the walker and rendering a comparison of reaction times moot. In the detection paradigm (Figure 4b), subjects showed significantly better performances for the inverted than for the upright human photos (F(1, 5) = 9.832, P = 0.002). We conclude that inversion diminishes the interference effect for pictures of humans, like it did for stick figures in Experiment 1.

Experiment 3: No categoryspecific interference in a different task of object recognition

In the previous experiments, the local objects of the different categories were matched for low-level properties such as form, outline, and complexity. However, it is still possible that humans represent a special category different to all the others. In that case, one would expect that human forms should also interfere more strongly than other categories if the global level does not represent a human. This experiment tested whether the similarity between distractor (human figure) and test stimulus (walker) is relevant, or whether human figures are generally more disruptive than other objects simply because they are more salient.

Methods

This experiment presented static letters or numbers that were composed of local elements of the object categories humans, tools, vegetables, animals, vehicles, points, and abstract tools, similar to typical Navon stimuli (see Figure 5). Ten letters and ten numbers (A, b, C, E, f, I, j, K, N, S and 0, 1, 2, 3, 4, 5, 6, 7, 8, 9) were used. The task was to decide, as fast as possible, if the presented stimulus was a letter or a number. The answers were given with the arrow keys, left and right. Ten subjects (four males) between 22 and 41 years old (average 32.09) participated. All subjects had normal or corrected-tonormal vision and were naive to the purpose of the experiment. Like in the other experiments, subjects were explicitly told that the objects were irrelevant and that they should only concentrate on the task of number/letter discrimination.

The height and width of the stimuli depended somewhat on the form and the size of the constituting elements. The



Figure 4. Experiment 2: Results for the global upright humans walker. As in Figure 2, (a) the bar chart shows the results for the reaction time paradigm and (b) the line graph on the right shows the results for the detection paradigm.



Figure 5. Examples for stimuli used in Experiment 3. Subjects had to discriminate letters from numbers, each composed of images from the different object categories. (a) The number 2 consisting of pictures of humans. (b) The letter E consisting of vegetables.

maximum dimensions of the stimulus were 10.3×6.0 cm $(10.24^{\circ} \times 6.00^{\circ}$ viewing angle).

First, all possible letters and numbers were shown consisting of small dots to familiarize subjects with the stimuli. Thereafter, subjects performed 60 practice trials (one block) with these dot stimuli. Then, each subject performed two practice blocks (120 trials) with stimuli made up from objects intermixed from different categories. Finally, each subject performed 6 experimental blocks of 60 trials, one for each object category. These blocks were presented in randomized order. The entire experiment took about 15 min.

Results

We measured reaction times in speeded performance of this task. For data analysis, we used the same procedures as in the previous experiments. The results are shown in Figure 6. There was no difference in reaction speeds between any of the conditions (F(5, 44) = 0.908; P = 0.485). We conclude that human figures are not more disruptive than objects in a general form recognition task, that is not related to biological motion recognition.

Discussion

Processing of additional irrelevant objects impairs the perception of biological motion. This effect is especially pronounced if the irrelevant objects consist of human forms. Inversion of the human forms diminishes their effect on biological motion processing.

Hunt and Halper (2008) suggested that "the impaired recognition of walkers of different complex objects is consistent with evidence demonstrating a role for serial, attention-based processes". Accordingly, they proposed that attending to local elements would interfere with a global walker discrimination task and attending to the global elements would interfere with local discrimination. In our experiment, we told the subjects that the local objects are irrelevant and that instead they only had to concentrate on the global task. Because of this instruction, we would expect that the subjects attended to the global walker more than to the local objects. Nonetheless, it is possible that local objects differ in their salience and thereby in their ability to catch attention. We thus conducted an experiment that used the same categories as Experiment 1 in an object recognition task that did not involve biological motion. If salience is the reason for the worse performance with the human walker, we would also expect to find this category-specific interference in a different task of object recognition. The data of Experiment 3 showed no significant differences. Thus, we conclude that the effect we found is caused by the similarity between local human figures and global walker, and thus by interference of task-irrelevant information of the same semantic category.

Interference of irrelevant information in a cognitive task is often taken as evidence that the interfering information taps into processing capacities that are required to perform the task (Chan & Newell, 2008; Tresch, Sinnamon, & Seamon, 1993). In line with this, our results indicate that biological motion perception shares processing capacities with object recognition, particularly concerning the human form.

Our results thus support the view that biological motion perception requires the processing of specific knowledge



Figure 6. Experiment 3: Subjects had to decide as quickly as possible if the stimulus was a letter or a number. We tested six different conditions, each representing another object category. The used pictures of objects were the same as in the main experiment. The graph shows reaction speed and standard error.

about the human body. Conceptual knowledge is organized by semantic categories. Specific semantic category deficits have been found for animals, plants, and artifacts (Caramazza & Mahon, 2003) and also for the human body (Coslett et al., 2002).

People generally take longer to categorize objects into more abstract categories than into categories at the basic level of categorization (Rosch, Mervis, Gray, Johnson, & Boyes-Braem, 1976). The composition of objects placed at the joints of the walkers in Experiment 1 can be regarded as slightly more abstract than the basic level. The presented "humans" were from the basic categories "female," "male," "child," and "baby"; the "vehicles" were from basic categories such as "car," "boat," "fork lift," etc. Each walker was thus composed of objects of related basic categories and therefore represented a superordinate category. Still, one might argue that the "human" basic categories are more related than other categories that we used. However, had the level of categorization played a role in our experiments, we would have expected a different pattern of results. For broader categories of the local elements, the interference effect should be higher than for more narrow categories, because of the great variability. Considering the findings of Rosch et al. (1976), one would then expect that the processing of local objects of superordinate categories should be slower compared to local objects of basic categories. However, we found the greatest interference effect (slowest reaction speed) for the human forms, which are defined on a more basic categorization level. The comparatively bad performance for human forms is mediated by semantic affiliation to the same category and not by levels of categorization.

An important issue is at which level of processing the interference of the local figures with the global biological motion takes place. As described in the Methods section, the local figures of the different categories were carefully matched in size, orientation, outline, and complexity. Moreover, the movement pattern of the local figures was the same in all conditions, because these movements were determined by the joint motions at the global level. If the movement trajectories of the local objects would have been crucial to solve the task, we had expected to find no differences between the conditions. That these low-level aspects were matched across categories reduces the likelihood that the interference effects reflect low-level processes.

Positive evidence that we are studying high-level interference effects is provided by the conditions with inverted local figures. Since inverted figures contain the same low-level features as their upright counterparts, such as color or form, it is widely accepted that so-called inversion effects represent high-level processes. Our results thus provide positive evidence for high-level processes from the inversion effects, because the upright photographs caused greater interference than the inverted ones.

The observation that an inversion of the local human shapes restores the ability to process the global walker is consistent with the category-based interference. Inverted pictures of bodies look less like humans than upright pictures (Reed et al., 2003). Yet, the visual features of the inverted bodies (color, orientation, size, etc.) remain the same, as does the motion of each individual object. Hence, the impairment that is observed for upright body pictures must result from their nature as human bodies and not from any particular visual feature, or their motion. This is consistent with a global shape match for the recognition of human bodies and biological motion. Thus, the form processing of body shape is crucial for the recognition of the walker (Lange, Georg, & Lappe, 2006; Lange & Lappe, 2006).

Our experiments do not address the question of how many higher processing levels exist, and how they are connected. It is possible, for example, that on one level the visual input is compared with stored body templates before; on another level, a global percept of action is created from the gradually changing percept of the body. It is also possible that high-level knowledge about the body and its capability of movement is used in perception (Shiffrar & Freyd, 1990, 1993; Tadin, Lappin, Blake, & Grossman, 2002) or that motor knowledge from the mirror neuron system is recruited (Rizzolatti & Craighero, 2004; Serino et al., 2010). Parts of the mirror neuron system including the premotor cortex are known to be activated by biological motion stimuli (de Lussanet et al., 2008; Michels, Kleiser, de Lussanet, Seitz, & Lappe, 2009; Michels et al., 2005; Saygin, Wilson, Hagler, Bates, & Sereno, 2004; Vaina et al., 2001) and might contribute to the perception of biological motion. Since premotor cortex is also known to be activated to a small degree by static images of implied actions (de Lafuente & Romo, 2004; Urgesi, Moro, Candidi, & Aglioti, 2006), the interference of the human category with the global walker processing might be related to interference in the mirror neuron system. Premotor cortex is also activated by views of tools (Chao & Martin, 2000; Grabowski, Damasio, & Damasio, 1998). This finding may offer an intriguing explanation for the observed interference of the tools category in the detection paradigm. However, the tools category did not interfere strongly in the reaction time paradigm. Thus, the link to the mirror system should be seen as speculative at the moment.

Moreover, it seems possible that implied motion can affect the perception of biological motion, because of shared processing capacities in the motion system. Indeed, Kourtzi and Kanwisher (2000) showed that static images of the human form may activate motion-related brain areas if they imply motion. They tested images of athletes with implied motion, images of athletes without implied motion, and images of people at rest. They found that implied motion, but not the two other categories, activate motion-related brain regions. For our experiments, we selected images of humans and animals, in static poses that do not imply motion under the definitions used by Kourtzi and Kanwisher (2000). The shape matching with the other object categories required in some occasion poses that originated from gymnastics and that, therefore, indicated actions. However, the poses were chosen such that the body was in stable support and would be hold in that pose for some time, thus not implying ongoing motion Therefore, we think it unlikely that the interference effects are related to implied motion processes in the brain. Moreover, pictures of animals can imply motion in the same way as pictures of humans (Kourtzi & Kanwisher, 2000). Therefore, if motion processes would be involved in the interference effects, it should have affected the human and animal categories alike, which was not the case. Thus, independently of the question of how many higher processing levels exist and how they are connected, the data cannot be explained by implied motion.

The walkers composed of human shapes can be regarded as a special class of Navon figures, complex global shapes that are composed of small local elements of similar shapes, for instance the letter "T" composed of linear arrangements of small letters "F" (Navon, 1977). Navon proposed a precedence for the perception of the global level because he found that mismatches between the stimuli at the two levels interfere only with processing of the local level, not the global level. Later research, however, showed that global and local processing pass off in parallel (Blanca, Luna, Lopez-Montiel, Zalabardo, & Rando, 2002; Hoffman, 1980). Our results, viewed from that perspective, suggest that human-walker perception on the global level suffers from interference from the local level. This remarkable inversion of the global preference shows that the influence of object recognition on biological motion is very strong. Based on experiments with Navon figures composed of objects or non-objects, Poirel, Pineau, and Mellet (2006) proposed two processes passing by in parallel: automatic identification and structural analysis. Identification of objects happens automatically and independent of the relevance for the task. Consistent with this, performance differences between the conditions in our experiment occurred even though the subjects were explicitly told that they should ignore the objects and only concentrate on the task. We conclude that human shapes cause an interference with biological motion recognition because the analysis of human form is an automatic and crucial part of the process of biological motion perception. Likewise, the presence of objects at the local level interferes with biological motion processing because the recognition of human form and object form shares partly the same resources in the brain.

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References

- Beintema, J. A., Georg, K., & Lappe, M. (2006). Perception of biological motion from limited lifetime stimuli. *Perception & Psychophysics*, 68, 613–624.
- Beintema, J. A., & Lappe, M. (2002). Perception of biological motion without local image motion. *Proceedings of the National Academy of Sciences of the United States of America*, 99, 5661–5663.
- Blanca, M. J., Luna, R., Lopez-Montiel, D., Zalabardo, C., & Rando, B. (2002). Effect of the similarity between target and global and local levels in hierarchical stimuli processing. *Psychological Research*, 66, 124–132.
- Bonda, E., Petrides, M., Ostry, D., & Evans, A. (1996). Specific involvement of human parietal systems and the amygdala in the perception of biological motion. *Journal of Neuroscience*, *16*, 3737–3744.
- Caramazza, A., & Mahon, B. Z. (2003). The organization of conceptual knowledge: The evidence from category-specific semantic deficits. *Trends in Cognitive Sciences*, 7, 354–361.
- Chan, J. S., & Newell, F. N. (2008). Behavioral evidence for task-dependent "what" versus "where" processing within and across modalities. *Perception & Psychophysics*, 70, 36–49.
- Chang, D. H. F., & Troje, N. F. (2008). Perception of animacy and direction from local biological motion signals. *Journal of Vision*, 8(5):3, 1–10, http://www. journalofvision.org/content/8/5/3, doi:10.1167/8.5.3. [PubMed] [Article]
- Chao, L. L., & Martin, A. (2000). Representation of manipulable man-made objects in the dorsal stream. *Neuroimage*, *12*, 478–484.
- Coslett, H. B., Saffran, E. M., & Schwoebel, J. (2002). Knowledge of the human body: A distinct semantic domain. *Neurology*, *59*, 357–363.
- de Lafuente, V., & Romo, R. (2004). Language abilities of motor cortex. *Neuron*, *41*, 178–180.
- de Lussanet, M. H. E., Fadiga, L., Michels, L., Seitz, R. J., Kleiser, R., & Lappe, M. (2008). Interaction of visual hemifield and body view in biological motion perception. *European Journal of Neuroscience*, 27, 514–522.
- Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science*, 293, 2470–2473.

- Giese, M. A., & Poggio, T. (2003). Neural mechanisms for the recognition of biological movements. *Nature Reviews, Neuroscience, 4,* 179–192.
- Grabowski, T. J., Damasio, H., & Damasio, A. R. (1998). Premotor and prefrontal correlates of category-related lexical retrieval. *Neuroimage*, 7, 232–243.
- Grossman, E. D., & Blake, R. (2002). Brain areas active during visual perception of biological motion. *Neuron*, 35, 1167–1175.
- Grossman, E. D., Donnelly, M., Price, R., Pickens, D., Morgan, V., Neighbor, G., et al. (2000). Brain areas involved in perception of biological motion. *Journal* of Cognitive Neuroscience, 12, 711–720.
- Hoffman, J. E. (1980). Interaction between global and local levels of a form. *Journal of Experimental Psychology. Human Perception and Performance*, 6, 222–234.
- Hunt, A. R., & Halper, F. (2008). Disorganizing biological motion. *Journal of Vision*, 8(9):12, 1–5, http://www. journalofvision.org/content/8/9/12, doi:10.1167/ 8.9.12. [PubMed] [Article]
- Johansson, G. (1973). Visual perception of biological motion and a model for its analysis. *Perception & Psychophysics*, 14, 201–211.
- Kourtzi, Z., & Kanwisher, N. (2000). Activation in human MT/MST by static images with implied motion. *Journal of Cognitive Neuroscience*, *12*, 48–55.
- Lange, J., Georg, K., & Lappe, M. (2006). Visual perception of biological motion by form: A templatematching analysis. *Journal of Vision*, 6(8):6, 836–849, http://www.journalofvision.org/content/6/8/6, doi:10.1167/6.8.6. [PubMed] [Article]
- Lange, J., & Lappe, M. (2006). A model of biological motion perception from configural form cues. *Journal* of Neuroscience, 26, 2894–2906.
- Michels, L., Kleiser, R., de Lussanet, M. H. E., Seitz, R. J., & Lappe, M. (2009). Brain activity for peripheral biological motion in the posterior superior temporal gyrus and the fusiform gyrus: Dependence on visual hemifield and view orientation. *Neuroimage*, 45, 151–159.
- Michels, L., Lappe, M., & Vaina, L. M. (2005). Visual areas involved in the perception of human movement from dynamic form analysis. *Neuroreport*, 16, 1037–1041.
- Navon, D. (1977). Forest before trees: The precedence of global features in visual perception. *Cognitive Psychology*, 9, 353–383.
- Pavlova, M., & Sokolov, A. (2000). Orientation specificity in biological motion perception. *Perception & Psychophysics*, 62, 889–899.

- Peelen, M. V., & Downing, P. E. (2005a). Is the extrastriate body area involved in motor actions? *Nature Neuroscience*, *8*, 125.
- Peelen, M. V., & Downing, P. E. (2005b). Selectivity for the human body in the fusiform gyrus. *Journal of Neurophysiology*, 93, 603–608.
- Poirel, N., Pineau, A., & Mellet, E. (2006). Implicit identification of irrelevant local objects interacts with global/local processing of hierarchical stimuli. *Acta Psychologica*, *122*, 321–336.
- Reed, C. L., Stone, V. E., Bozova, S., & Tanaka, J. (2003). The body-inversion effect. *Psychological Science*, *14*, 302–308.
- Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, 27, 169–192.
- Rosch, E., Mervis, C. B., Gray, W. D., Johnson, D. M., & Boyes-Braem, P. (1976). Basic objects in natural categories. *Cognitive Psychology*, 8, 382–439.
- Saygin, A. P., Wilson, S. M., Hagler, D. J. J., Bates, E., & Sereno, M. I. (2004). Point-light biological motion perception activates human premotor cortex. *Journal* of Neuroscience, 24, 6181–6188.
- Serino, A., De Filippo, L., Casavecchia, C., Coccia, M., Shiffrar, M., & Ladavas, E. (2010). Lesions to the motor system affect action perception. *Journal of Cognitive Neuroscience*, 22, 413–426.
- Shiffrar, M., & Freyd, J. (1990). Apparent motion of the human body. *Psychological Science*, 1, 257–264.
- Shiffrar, M., & Freyd, J. (1993). Timing and apparent motion path choice with human body photographs. *Psychological Science*, *4*, 379–384.
- Singer, J. M., & Sheinberg, D. L. (2010). Temporal cortex neurons encode articulated actions as slow sequences of integrated poses. *Journal of Neuroscience*, *30*, 3133–3145.
- Sumi, S. (1984). Upside-down presentation of the Johansson moving light pattern. *Perception*, *13*, 283–286.
- Tadin, D., Lappin, J. S., Blake, R., & Grossman, E. D. (2002). What constitutes an efficient reference frame for vision? *Nature Neuroscience*, 5, 1010–1015.
- Thompson, J. C., Clarke, M., Stewart, T., & Puce, A. (2005). Configural processing of biological motion in human superior temporal sulcus. *Journal of Neuroscience*, 25, 9059–9066.
- Tresch, M. C., Sinnamon, H. M., & Seamon, J. G. (1993). Double dissociation of spatial and object visual memory: Evidence from selective interference in intact human subjects. *Neuropsychologia*, *31*, 211–219.
- Urgesi, C., Moro, V., Candidi, M., & Aglioti, S. M. (2006). Mapping implied body actions in the human motor system. *Journal of Neuroscience*, *26*, 7942–7949.

- Vaina, L. M., Solomon, J., Chowdhury, S., Sinha, P., & Belliveau, J. W. (2001). Functional neuroanatomy of biological motion perception in humans. *Proceedings* of the National Academy of Sciences of the United States of America, 98, 11656–11661.
- Vangeneugden, J., Pollick, F., & Vogels, R. (2008). Functional differentiation of macaque visual temporal

cortical neurons using a parametric action space. *Cerebral Cortex, 19,* 593-611.

van Zandt, T. (2002). Analysis of response time distributions. In H. Pashler & J. Wixted (Eds.), *Steven's handbook of experimental psychology* (vol. 4, chap. 12, pp. 461–516). New York: Wiley and Sons.