

# Movement in Aesthetic Experiences: What We Can Learn from Parkinson Disease

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#### **Abstract**

■ Visual art offers cognitive neuroscience an opportunity to study how subjective value is constructed from representations supported by multiple neural systems. A surprising finding in aesthetic judgment research is the functional activation of motor areas in response to static, abstract stimuli, like paintings, which has been hypothesized to reflect embodied simulations of artists' painting movements, or preparatory approach—avoidance responses to liked and disliked artworks. However, whether this motor involvement functionally contributes to aesthetic appreciation has not been addressed. Here, we examined the aesthetic experiences of patients with motor dysfunction. Forty-three people with Parkinson disease and 40 controls made motion and aesthetics judgments of high-motion Jackson Pollock paintings and low-motion Piet Mondrian paintings. People with Parkinson disease demonstrated stable and internally consistent

preferences for abstract art, but their perception of movement in the paintings was significantly lower than controls in both conditions. The patients also demonstrated enhanced preferences for high-motion art and an altered relationship between motion and aesthetic appreciation. Our results do not accord well with a straightforward embodied simulation account of aesthetic experiences, because artworks that did not include visual traces of the artist's actions were still experienced as lower in motion by Parkinson patients. We suggest that the motor system may be involved in integrating low-level visual features to form abstract representations of movement rather than simulations of specific bodily actions. Overall, we find support for hypotheses linking motor responses and aesthetic appreciation and show that altered neural functioning changes the way art is perceived and valued.

### INTRODUCTION

Visual art offers cognitive neuroscience an opportunity to study how subjective value is constructed from interactions between multiple neural systems. Experiments in neuroaesthetics suggest that aesthetic experiences engage separable neural systems that represent perceptual and motor information, emotion and value, and semantic knowledge; a model known as the aesthetic triad (Chatterjee & Vartanian, 2014). Whereas most experiments have studied static works of art such as paintings, functional activation of motor areas of the brain has often been found, particularly in response to paintings experienced as especially "dynamic." Several hypotheses about the nature of this motor activity have been proposed. Some have argued for an embodied simulation account of aesthetic experience, according to which observers simulate the movements and experiences of the painting's subject or its artist (Freedberg & Gallese, 2007), whereas others have suggested that motor activity might reflect preparatory approach-avoidance responses to liked and disliked artworks (Ishizu & Zeki, 2011; Kawabata & Zeki, 2004). However, the extent to which motor involvement functionally contributes to aesthetic appreciation or is merely an epiphenomenal byproduct

of other processing is not well understood. To address this question, we examined whether motor system dysfunction alters the aesthetic experiences of patients with Parkinson disease. Our study addresses the question of motor involvement in aesthetic valuation generally, as well as in Parkinson disease specifically.

Both visual motion and motor responses to art have been reported. Studies reporting the former typically used as stimuli artworks that depicted figures or objects in states of implied motion. Activation of the middle temporal visual motion area (MT+) was found in response to implied motion in van Gogh paintings (Thakral, Moo, & Slotnick, 2012), Hokusai Manga (Osaka, Matsuyoshi, Ikeda, & Osaka, 2010), and the dynamic works of Futurism and Cubism (Kim & Blake, 2007). Some studies reporting motor cortex responses to visual art also used representational paintings as stimuli. Corticomotor excitability of an arm muscle was increased when observers viewed a posture involving that muscle in Michaelangelo's Expulsion from Paradise, but not when the viewing the same muscle at rest in other paintings (Battaglia, Lisanby, & Freedberg, 2011). In a study using similar stimuli, connectivity between dorsal premotor cortex and primary motor cortex was increased when viewing a painting with implied action postures compared to one with static, resting postures (Concerto et al., 2016).

Although interesting, these results are not specific to aesthetics or visual art perception. They replicate earlier

findings from cognitive neuroscience regarding the neural bases of action observation and visual motion perception. The finding that area MT+ is responsive to implied motion in static images was first reported in studies using nonart images of bodies and objects with implied motion (Kable, Kan, Wilson, Thompson-Schill, & Chatterjee, 2005; Kable, Lease-Spellmeyer, & Chatterjee, 2002; Kourtzi & Kanwisher, 2000; Senior et al., 2000). Similarly, premotor and primary motor cortex were shown to respond to static images of human actions (Proverbio, Riva, & Zani, 2009; Urgesi, Moro, Candidi, & Aglioti, 2006).

A separate line of research suggests that observers are sensitive to the movement information carried in visible brushstrokes in paintings. Features of an artist's original movement, such as trajectory and force, may be preserved in the gestural quality of their brushstrokes, and observers perhaps simulate the parent action from the information contained in its trace (Freedberg & Gallese, 2007). In one study, participants made faster arm movements when the direction of their movement was compatible with the direction of task-irrelevant brushstrokes (Taylor, Witt, & Grimaldi, 2012). In an electroencephalography, greater mu rhythm suppression was evoked by Lucio Fontana's slashed canvases compared to control stimuli, which contained similar shapes to the originals but lacked the depth information suggestive of Fontana's cutting actions (Umiltà, Berchio, Sestito, Freedberg, & Gallese, 2012). Similarly, greater activity in motor cortical areas was found when observers viewed Franz Kline's gestural paintings compared to control images in which the movement information was removed (Sbriscia-Fioretti, Berchio, Freedberg, Gallese, & Umiltà, 2013). Importantly, the paintings used as stimuli in these studies were abstract and did not contain any representational depictions of action or implied motion. Thus, observers are thought to be responsive to visual cues in the way the paint was applied (or the canvas was cut) that imply intentional movements of the artist. However, the fact that motor information can be inferred from the results or traces of movements is, again, not specific to aesthetics. For example, greater activity in motor and premotor cortex was found when observers viewed handwritten letters compared to printed letters (Longcamp, Tanskanen, & Hari, 2006), which was lateralized according to handedness (Longcamp, Anton, Roth, & Velay, 2005). Authorship effects were also observed, where participants more accurately predicted handwriting strokes from parts of self-produced relative to other-produced trajectories (Knoblich, Seigerschmidt, Flach, & Prinz, 2002).

For research on motor (or visual motion) responses to art to have something to say about aesthetics, beyond replicating and generalizing nonaesthetic findings to an art context, these motor/motion responses must demonstrably shape the subjective value or meaning one assigns to the object. However, aesthetic responses were often not measured in prior research on this topic (Concerto et al., 2016; Battaglia et al., 2011; Osaka et al., 2010; Kim & Blake, 2007). Some studies that did measure aesthetic

responses showed that, in addition to greater motor activity, paintings with implied movement were associated with higher motion and liking ratings relative to control images (Sbriscia-Fioretti et al., 2013; Umiltà et al., 2012), but did not explicitly show a relationship between motion and appreciation. The control stimuli used in these studies were nonart images, and the paintings may have been liked more because of their status as art objects rather than their movement content.

Other works linking motion to aesthetic appreciation provide conflicting evidence on whether this association is positive or negative. Mastandrea and Umiltà (2016) found a positive correlation between the amount of perceived motion in a painting and aesthetic appreciation. Thakral et al. (2012) showed that greater MT+ responses to high motion paintings were greater still when the painting was liked. The most direct evidence of a relationship between motor representations and aesthetic appreciation comes from Leder, Bär, and Topolinski (2012) and Ticini, Rachman, Pelletier, and Dubal (2014), both of which trained participants to make pointillist and stroke style movements with a paintbrush. In Ticini et al. (2014), liking of pointillist paintings was subsequently enhanced when the paintings were primed with congruent images of appropriate hand grips for making pointillist movements. In Leder et al. (2012), participants who made pointillist movements while viewing artworks gave higher liking to point-style relative to stroke-style art, whereas the opposite pattern was found for participants who made stroke movements while viewing artworks. In addition, a recent facial feedback study found that when participants were asked to overtly frown, they gave higher aesthetic ratings to artworks depicting painful facial expressions than when they kept their face muscles relaxed (Ardizzi et al., 2020). Finally, in a nonart but nevertheless aesthetic context, it was found that people have unconscious motor approach responses toward incidental beautiful faces (Faust, Chatterjee, & Christopoulos, 2019).

In contrast, other studies suggest a complicated relationship between motion and aesthetic preference. Across a series of studies, compared to neutral paintings, activity in left motor cortex increased in response to paintings classed as ugly and decreased in response to paintings classed as beautiful (Ishizu & Zeki, 2011; Kawabata & Zeki, 2004). Similarly, sculptures judged as ugly elicited significantly greater activity in motor cortex than those judged as beautiful (Di Dio, Macaluso, & Rizzolatti, 2007). Moreover, increasing excitatory activity in motor cortex and inhibitory activity in medial orbitofrontal cortex with transcranial direct current stimulation caused significant decreases in beauty ratings given to artworks (Nakamura & Kawabata, 2015). Based on these findings, Kawabata and Zeki (2004) proposed that perceiving salient visual stimuli mobilizes the motor system to take some action toward or away from rewarding and aversive objects. Perhaps ugly art is avoided like any other aversive stimulus, but some beautiful art, as an example of a stimulus category that evokes "liking

without wanting" (Chatterjee, 2013), does not necessarily evoke approach responses. Previously, it was shown that judgments of facial beauty can be made in the absence of approach motivations (Aharon et al., 2001). In addition, the most moving aesthetic experiences have not been linked to action but rather to the brain's default mode network, a task-negative network associated with rest, mind wandering, and self-referential thought (Vessel, Isik, Belfi, Stahl, & Starr, 2019; Belfi et al., 2019; Vessel, Starr, & Rubin, 2012, 2013; although see Menninghaus et al., 2019, for a description of how aesthetic emotions are expressed as bodily movements).

Although embodied simulation and approach—avoidance mechanisms are offered as explanations of motor responses to art, it is not known whether motor involvement functionally contributes to aesthetic experiences or occurs alongside them without shaping judgment. If motor involvement does functionally contribute to aesthetic appreciation, this process should be disrupted in Parkinson disease patients with neurological motor dysfunction. Although the primary pathophysiology of Parkinson disease is the loss of dopaminergic neurons in the basal ganglia, dopamine depletion alters regional metabolism, electrophysiological activity, and functional activation of motor cortex (Burciu & Vaillancourt, 2018; Lindenbach & Bishop, 2013; Galvan & Wichmann, 2008).

Parkinson disease has previously been linked to impairments in representing or simulating actions in motor imagery (van Nuenen et al., 2012; Helmich, de Lange, Bloem, & Toni, 2007), action observation (Poliakoff, 2013), gesture (Humphries, Holler, Crawford, Herrera, & Poliakoff, 2016), and language (Bocanegra et al., 2017; Fernandino et al., 2013), although language effects predicted by simulation accounts are not always consistently observed (Humphries et al., 2019). One other study to date has examined changes in aesthetic appreciation in people with Parkinson disease (Lauring et al., 2019). In this study, participants completed the Assessment of Art Attributes (Chatterjee, Widick, Sternschein, Smith, & Bromberger, 2010) along with liking and beauty ratings on a set of 15 paintings. People with Parkinson disease rated the artworks as higher in emotionality, but otherwise gave similar ratings to controls. Critically, this study did not investigate the relationship between motor and aesthetic responses, and therefore did not include a motion rating.

To test the hypothesis that the brain's motor system functionally contributes to aesthetic experiences, we examined whether aesthetic judgments, motion ratings, and the relationships between them were altered in patients with neural motor dysfunction. Participants were exposed to two sets of abstract paintings. The first set, dominated by intensely dynamic movement, were action paintings by Jackson Pollock (the "high-motion" condition). The second set, characterized by the meticulous use of straight lines, color blocking, and an absence of gestural strokes, were neoplastic paintings by Piet Mondrian (the "low-motion" condition). Our hypothesis

led to the following testable predictions for the relationship between motor system integrity, motion, and aesthetic valuation.

- 1. If motion perception is not involved in aesthetic valuation, then no systematic relationship will be found between people's motion and valuation ratings.
- If general dysfunction of striatal reward and executive processing results in disruptions in aesthetic appreciation, then people with Parkinson disease will have altered or erratic aesthetic valuations that are not associated directly with or specific to motion characteristics of artwork.
- 3. If the motor system typically allows one to understand and appreciate the artist's actions and intentions as expressed in motion in artwork (see embodied simulation account: Freedberg & Gallese, 2007), then people with Parkinson disease will have altered aesthetic valuations of art work as related to art's motion characteristics.
  - a. If people with Parkinson disease are unable to form movement representations, their valuations of artwork as related to motion will be erratic and different than controls.
  - b. If people with Parkinson disease can form movement representations, but these representations are altered systematically, their valuations of artworks as related to motion will be internally consistent but different than controls.

#### **METHODS**

#### **Participants**

Forty-three Parkinson disease patients were recruited from the Parkinson Disease and Movement Disorders Center at Pennsylvania Hospital. Forty control participants, matched to the patients on age and education, were recruited from two elderly control research databases maintained by the Penn Center for Cognitive Neuroscience and the Penn Memory Center. Participants were eligible if they were classed as cognitively unimpaired (i.e., not meeting criteria for a diagnosis of dementia or mild cognitive impairment). The Parkinson disease participants were part of a long-term cohort study tracking the development of their symptoms over several years and thus underwent regular cognitive examinations. Patients classed as cognitively unimpaired at the most recent neurologists' consensus meeting were invited to participate. All participants were also screened for cognitive impairment at the testing session using the Montreal Cognitive Assessment, which examines attention, memory, language, executive function, and visuospatial skills (Nasreddine et al., 2005). Participants were excluded if they had a diagnosis of any other neurological disease other than Parkinson disease, if they had ever had a stroke or a traumatic brain injury, if they had undergone deep brain stimulation, or if they had

**Table 1.** Participant Demographics and Clinical Features of the Parkinson Disease Group

	Parkinson	Control
Age, years	67.84 (8.13)	69.5 (7.77)
Education, years	16.91 (2.0)	17.4 (3.16)
Sex	23 M, 20 F	14 M, 26 F
Montreal Cognitive Assessment (max 30)	28.12 (1.48)	28.03 (1.52)
Disease duration (years)	7.79 (4.13)	
Unified Parkinson Disease Rating Scale - motor subscale	23.76 (9.46)	
Levodopa equivalent dose	701.86 (404.89)	
Hoehn and Yahr stage	Stage $1 = 1$	
	Stage $2 = 29$	
	Stage $3 = 12$	
	Stage $4 = 0$	
	Stage $5 = 1$	

Mean (SD) unless otherwise specified.

an uncorrected visual impairment. Demographic and clinical features of the participant groups are reported in Table 1.

# **Materials and Norming**

High-resolution photographs of 10 action paintings by Jackson Pollock and 10 neoplastic paintings by Piet Mondrian were used as materials in two experimental tasks (listed in the Appendix of this paper). The selected paintings

were drawn from a larger set of 34 Pollock paintings and 40 Mondrian paintings, which were normed online. Fifty raters were recruited using Amazon's Mechanical Turk platform to view and rate the paintings, which were presented using Qualtrics. The raters' mean age was 34.16 years (min = 22, max = 59), and their mean education was 14.66 years (min = 10, max = 20). We did not require the raters to be experts or naïve about art, but most were naïve (as measured by the Art Experience Questionnaire; Chatterjee et al., 2010). Of the 50 raters, 41 visited art museums once a year or almost never, and eight correctly recognized Pollock and/or Mondrian as the artists of the paintings they saw. On average, the raters spent less than 1 hr per week either making, reading about, or looking at visual art. Participants viewed the paintings in a random order and rated them on nine dimensions using 7-point Likert scales. Four dimensions referred to personal and evaluative experiences of the paintings (liking, beauty, interest, and familiarity), and five dimensions referred to formal features of the paintings (motion, complexity, balance, color-hue, and color-saturation).

The norming of the 34 Pollocks and 40 Mondrians revealed substantial differences between the two groups of paintings. Critically and consistent with our assumptions about the action paintings, the Pollocks were rated significantly and substantially higher for motion than the Mondrian paintings (see Table 2). In addition, the Pollocks were rated more beautiful, more interesting, more complex, and were liked more than the Mondrians, whereas the Mondrians were rated more balanced and more familiar than the Pollocks. The paintings did not differ in hue and saturation ratings.

From this larger set, 10 paintings from each artist were selected for use in this study. At the first stage of stimulus selection, paintings from the artists' earlier periods, which were more representational or figurative, were eliminated. From the remaining set, we selected paintings that

Table 2. Normative Ratings of a Large Set of 34 Pollocks and 40 Mondrians

Rating	Mondrian	Pollock	t	p	Cohen's d	95% Confidence Interval	
						Lower	Upper
Motion	2.33 (1.11)	5.41 (.98)	-16.66	<.001	-2.356	-3.461	-2.716
Familiarity	3.64 (1.53)	2.68 (1.21)	6.24	<.001	0.882	0.649	1.267
Beauty	3.50 (1.25)	3.85 (1.22)	-2.12	.039	-0.300	-0.693	-0.019
Interest	3.29 (1.28)	4.82 (1.18)	-8.53	<.001	-1.206	-1.892	-1.171
Liking	3.50 (1.36)	4.01 (1.27)	-2.90	.006	-0.410	-0.867	-0.157
Complexity	2.67 (.84)	5.35 (.75)	-17.47	<.001	-2.470	-2.985	-2.369
Balance	4.85 (.97)	4.01 (1.05)	4.10	<.001	0.580	0.425	1.241
Hue	3.98 (.56)	4.07 (.52)	-1.20	.238	-0.169	-0.261	0.066
Saturation	3.92 (.59)	4.06 (.59)	-1.46	.152	-0.206	-0.330	0.053

**Table 3.** Normative Ratings of the Experimental Set

Rating	Mondrian	Pollock	t	p	Coben's d	95% Confidence Interval	
						Lower	Upper
Motion	2.36 (.71)	5.51 (.64)	-10.41	<.001	-4.655	-3.793	-2.519
Familiarity	3.66 (.56)	2.80 (.31)	4.24	<.001	1.898	0.433	1.283
Beauty	3.58 (.45)	3.75 (.51)	-0.80	.436	-0.356	-0.619	0.279
Interest	3.38 (.85)	4.74 (.29)	-4.79	<.001	-2.141	-1.957	-0.763
Liking	3.63 (.55)	3.91 (.48)	-1.21	.243	-0.540	-0.768	0.208
Complexity	2.76 (1.08)	5.41 (.49)	-7.01	<.001	-3.136	-3.434	-1.850
Balance	4.91 (.35)	3.97 (.37)	5.78	<.001	2.583	0.597	1.279
Hue	3.63 (.75)	3.88 (.43)	-0.92	.372	-0.409	-0.824	0.324
Saturation	3.85 (1.17)	3.89 (.8)	-0.10	.919	-0.046	-0.988	0.896

maximized the difference between artists on the motion rating while minimizing the difference between artists on beauty and liking, to ensure that the choice and ratings tasks (described below) were equally difficult between conditions. If, for example, the Pollock condition contained paintings that were all highly liked, this could make forced-choice decisions more difficult relative to the Mondrian condition. By retaining the motion difference and minimizing the liking and beauty differences between conditions, we ensured that the conditions were wellmatched in difficulty and orthogonalized variables that may otherwise have been confounded. In the experimental set, the Pollocks continued to be rated higher than the Mondrians for motion, complexity, and interest; the Mondrians remained higher than the Pollocks for familiarity and balance; but the differences in beauty and liking were no longer significant (see Table 3 below).

#### **Procedure**

Participants were tested individually, and on their usual medication, either at home (16 patients, six controls) or at Pennsylvania Hospital or the Hospital of the University of Pennsylvania (27 patients, 34 controls). Home testing appointments were scheduled for times when participants could be sure that their home environment would be quiet and undisturbed (i.e., without social or family distractions). Hospital appointments were conducted in quiet testing rooms.

Participants were first shown the full set of 20 paintings to familiarize them with the works. The paintings were presented in a random order for each participant using E-Prime 3 (Psychology Software Tools). Each painting appeared on the screen for 5 sec and was preceded by a 1-sec fixation cross. Participants were instructed to simply look and pay attention to the images.

#### Two-Alternative Forced-Choice Task

Following the familiarization, participants completed a twoalternative forced-choice (2AFC) task that tested the internal consistency of their own preference judgments. Pairs of paintings within each artist were presented side by side. Participants indicated which painting they preferred. Each set of 10 paintings results in 45 possible pairs. Each of the 45 pairs was shown to the participants 3 times, for a total of 135 pairs of Pollocks and 135 pairs of Mondrians. There was no time limit on participants' choice decisions.

# Ratings Task

Finally, using 7-point Likert scales, participants rated the paintings along the same nine dimensions as in the norming study (personal-evaluative: liking, beauty, interest, familiarity; formal-composition: motion, complexity, balance, colorhue, color-saturation). The color dimensions served as relatively objective control ratings to check that the patients were able to rate sensibly. For this task, the paintings were again presented individually and in random order using E-Prime 3. The rating scales were presented one at a time underneath the paintings. Participants completed all nine ratings on each painting before moving to the next item. Instructions presented on screen at the beginning of the task made clear that participants were being asked for their opinion, that there were no correct or incorrect answers, and that there were no time restrictions for their responses. On each trial, participants used the mouse to click on the number corresponding to their rating and then pressed the spacebar to move to the next rating. Anchor points for 1 and 7 were labeled as follows:

Liking: How much do you like this image? 1 = not at all, 7 = very much.

Beauty: *How beautiful is this image?* 1 = not at all beautiful, 7 = very beautiful (instructions clarified

that liking and beauty ratings need not match up, i.e., it is possible to like a painting without finding it particularly beautiful and vice versa).

Interest: *How interesting is this image?* 1 = not at all interesting, 7 = very interesting.

Familiarity: How familiar is this image? 1 = not at all familiar, 7 = very familiar.

Motion: How much motion do you see or feel in this *image?* 1 = no motion, 7 = a lot of motion.

Complexity: *How complex is this image?* 1 = very simple, 7 = very complex.

Balance: How balanced is this image? 1 = very unbalanced, 7 = very balanced (instructions clarified that balance refers to a feeling of equality, stability, or harmony in how the visual weight of the image is distributed).

Hue: How warm or cool are the colors in this image? 1 = more cool, 7 = more warm (instructions clarifiedthat warm colors were red, orange, and yellow, and cool colors were green, blue, and purple).

Saturation: How calm or vibrant are the colors in this *image?* 1 = more calm, 7 = more vibrant (instructions clarified that calm colors were muted and washed out, and vibrant colors were vivid and bold).

# **Data Analysis**

2AFC Analysis

Subject-specific preference scores were calculated for each painting by dividing the number of times the painting was chosen by the number of times it was presented (27). For each participant, the paintings from each artist were then ranked in order from most preferred to least preferred. Paintings selected an equal number of times received tied ranks. These ranks were then used to identify transitivity violations, that is, when participants selected a less preferred painting over a more preferred painting, according to their own ranked order. The distance of each transitivity violation was also scored, which was the difference in rank between the two paintings. Decisions between tied ranks were not counted as violations. The number of transitivity violations per artist was counted for each participant, along with average violation distances. A 2 × 2 mixed ANOVA with Artist (Pollock/Mondrian) and Group (Parkinson disease/control) as fixed factors was used to analyze these data.

# Ratings Analysis

Item-level ratings were retained for each participant. Linear mixed-effects models were used to analyze these data, to account for variability in both participants and items. All participants participated in both artist conditions. We thus specified the mixed-effects models to include random intercepts for painting and by-subject random slopes for the Artist conditions. We analyzed the effect of Group, Artist, and their interaction on each rating separately, and the fixed and random effects structure was identical for each model:

Rating Dimension  $\sim$  Group  $\times$  Artist + (1|Painting) + (Artist|Subject)

Models were constructed using the *lme4* package in R (Version 3.6.3; The R Project for Statistical Computing) and p values were estimated using the *lmertest* package.

# **Data Availability**

The data reported in this study are openly available at https://osf.io/4qwaf/.

# **RESULTS**

# **2AFC Preference Transitivity**

The number of transitivity violations participants made in their forced-choice preference decisions was not significantly affected by Group, F(1, 81) = 0.15, p = .7,  $\eta_p^2 =$ .002; Artist, F(1, 81) = 2.01, p = .16,  $\eta_p^2 = .024$ ; or their interaction, F(1, 81) = 0.96, p = .33,  $\eta_p^2 = .012$ . The size of transitivity error distances was similarly not significantly affected by Group,  $F(1, 81) = 1.52, p = .22, \eta_p^2 = .018;$ Artist, F(1, 81) = 0.13, p = .72,  $\eta_p^2 = .002$ ; or their interaction, F(1, 81) = 2.04, p = .16,  $\eta_p^2 = .025$ . Transitivity means and standard deviations are reported in Table 4.

#### **Personal-Evaluative Ratings**

Familiarity ratings were not significantly affected by Group  $(\beta = 0.05, SE = 0.40, t = 0.12, p = .906)$ , Artist  $(\beta = 0.43, t = 0.43, t$ SE = 0.23, t = 1.86, p = .068), or their interaction ( $\beta =$ 0.23, SE = 0.24, t = 0.92, p = .358). The analysis of beauty ratings revealed a significant interaction between Group and Artist ( $\beta = 0.54$ , SE = 0.21, t = 2.50, p = .014), such that controls gave higher beauty ratings to the Mondrians than the Parkinson disease patients, whereas the Parkinson disease patients gave higher beauty ratings to the Pollocks than the controls. A very similar interaction between Group and Artist was also found for liking ratings  $(\beta = 0.6, SE = 0.24, t = 2.50, p = .015)$ , and for interest ratings ( $\beta = 0.62$ , SE = 0.21, t = 2.90, p = .005). Overall, controls preferred Mondrian paintings and Parkinson disease patients preferred Pollocks (ratings summarized in Figure 1 below).

#### **Formal-Composition Ratings**

For motion ratings, there was a significant main effect of Artist, confirming that the Pollock paintings were perceived as being higher in motion than the Mondrians

Table 4. Descriptive Statistics for the 2AFC Preference Transitivity Task

	Group	Transitivity	v Violations	Error Distance		
Artist		M	SD	$\overline{M}$	SD	
Mondrian	Control	8.85	4.99	1.72	0.61	
	Parkinson	8.58	5.11	1.54	0.35	
Pollock	Control	9.13	5.14	1.59	0.41	
	Parkinson	10.09	4.970	1.61	0.36	

(β = 2.32, SE = 0.41, t = 5.72, p < .001). There was also a significant main effect of Group (β = 0.82, SE = 0.26, t = 3.16, p = .002), such that Parkinson disease patients systematically gave lower motion ratings across both sets of paintings. There was no significant interaction between Group and Artist (β = 0.36, SE = 0.26, t = 1.38, p = .17).

Pollocks were rated higher in complexity than Mondrians ( $\beta = 1.73$ , SE = 0.45, t = 3.85, p < .001), but there was no significant effect of Group ( $\beta = 0.15$ , SE = 0.20, t = 0.77, p = .45) and no interaction ( $\beta = 0.09$ , SE = 0.22, t = 0.39, p = .70). No significant effects were found for Balance, Hue, or Saturation ratings (see Figure 1).

# Relationships between Motion, Appreciation, and Complexity

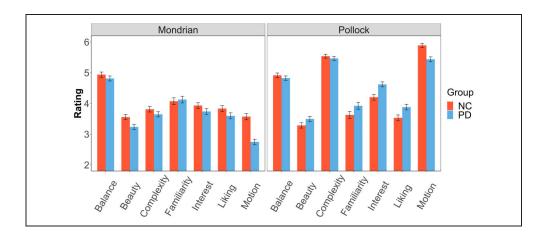
To summarize the results so far, we found that aesthetic appreciation was predicted by the interaction between Group and Artist. Across liking, beauty, and interest, the Mondrians were appreciated more by the controls than the Parkinson disease patients, whereas the Pollocks were appreciated more by the Parkinson disease patients than the controls. Motion was the only rating characterized by a significant main effect of Group, with Parkinson disease patients giving significantly lower motion ratings across the board. Next, we examined whether the relationship

between motion and appreciation was altered in Parkinson disease.

Given that ratings were recorded at the trial level (i.e., each participant's responses to each painting), a traditional correlation approach would not accurately capture the data structure. Averaging each participant's ratings across the paintings fails to capture variability in the paintings themselves. On the other hand, correlating at the level of the item does not account for the variance explained by participants. To account for both by-item and by-subject variance, we used the correlation package in R to analyze correlations between the ratings with a multilevel approach that included random effects for participant and painting. Note that N is large enough under this approach, given the number of data points (1597), that even weak correlations are statistically significant. Greater weight should be given to r than p values when evaluating the practical significance of these correlations.

Not surprisingly, the three evaluative ratings (liking, beauty, and interest) were all highly correlated with each other. Liked paintings were beautiful, r(1595) = .82, p < .001; beautiful paintings were interesting, r(1595) = .68, p < .001; and interesting paintings were liked, r(1595) = .77, p < .001. Motion and complexity ratings were not strongly correlated with each other, r(1595) = .33, p < .001, with complexity ratings accounting for only 10.89% of the variance in motion. Although the

**Figure 1.** Ratings of the paintings split by artist and group. NC = normal controls; PD = Parkinson disease.

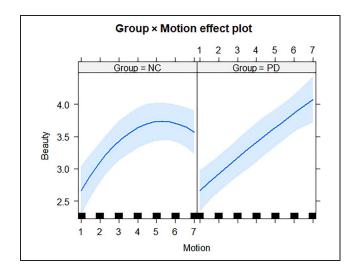


Pollock paintings were higher in both motion and complexity than the Mondrians, the minimal association between these variables suggests that effects observed in motion ratings are not driven by greater complexity. Correlation strengths are illustrated in Figure 2 below.

In addition, we examined whether the patients' motor symptom severity as measured by the Unified Parkinson Disease Rating Scale correlated with their perception of motion, r(40) = -.01, p = .99, or beauty, r(40) = -.04, p = .99, but found no significant relationships.

Next, we tested whether impairments in perceiving motion in the Parkinson disease group altered the relationship between motion and appreciation (beauty and liking). Although the linear correlation strengths between motion and liking, r(1595) = .2, p < .001, and motion and beauty, r(1595) = .2, p < .001, were low, scatterplots suggested that the relationships were quadratic rather than linear. For both beauty and liking as dependent variables, three mixed models were constructed to test the interaction between Group and Motion ratings, with motion's relationship to beauty and liking treated as 1) linear, 2) quadratic, and 3) cubic. Model comparisons revealed that both types of polynomial regression outperformed the linear regression, but the cubic model did not improve on the quadratic model. Here, we report the models with quadratic terms for motion.

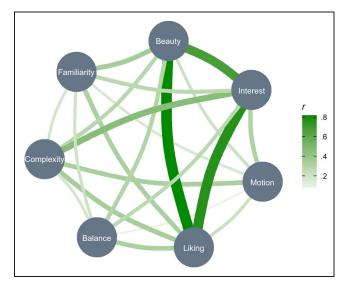
The interaction between Group and Motion significantly predicted beauty ( $\beta = 7.35$ , SE = 3.32, t = 2.22, p = .027) and liking ratings ( $\beta = 7.78$ , SE = 3.75, t = 2.08, p = .038). Figures 3 and 4 illustrate the results of these models. Controls demonstrate a quadratic relationship between motion and beauty/liking, where increases in motion at the low end are liked whereas increases in motion at the high end are disliked. This relationship is markedly different



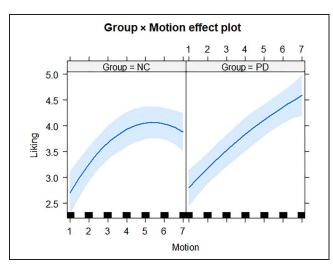
**Figure 3.** Fitted values from the model testing the effect of group and motion ratings on beauty ratings.

for Parkinson disease patients, who demonstrate a linear relationship between motion and beauty/liking.

To test the specificity of this relationship, we ran the same analysis procedure with complexity ratings instead of motion. Unlike the previous analyses with motion ratings, model comparisons revealed that including polynomial terms for complexity did not fit the data better than linear models, whereas the interaction between group and complexity also predicted beauty ( $\beta=0.13$ , SE=0.05, t=2.6, p=.009) and liking ( $\beta=0.15$ , SE=0.05, t=2.73, p=.006). Figure 5A and 5B illustrates that these relationships differed between groups in slope rather than in shape, with Parkinson disease patients demonstrating a slightly stronger relationship between complexity and appreciation.



**Figure 2.** Linear correlation strength between ratings. Control ratings of noninterest (hue and saturation) excluded for clarity.



**Figure 4.** Fitted values from the model testing the effect of Group and Motion ratings on liking ratings.

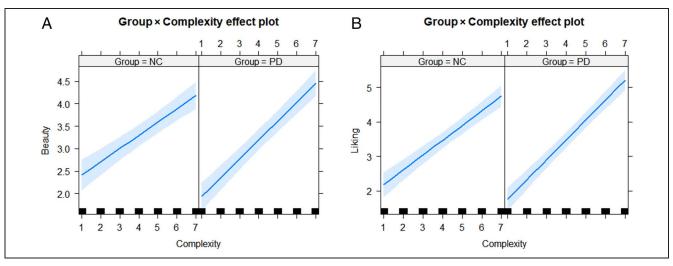


Figure 5. Fitted values from the models testing the effect of Group and Complexity ratings on (A) beauty and (B) liking ratings.

#### **DISCUSSION**

Motivated by the common observation that the motor system is engaged in response to visual art, this study tested the hypothesis that the motor system functionally contributes to aesthetic experiences. In a study sample that was large compared to typical patient samples in neuropsychology, we examined how motor system dysfunction in Parkinson disease affects aesthetic appreciation, the perception of movement in art, and the relationship between these variables. Our investigation provides several notable findings demonstrating that motor integrity of the viewer and motion characteristics of paintings contribute to aesthetic experiences.

At the most basic level, our data confirm the hypothesis that the perception of motion in art contributes to aesthetic experiences. People can infer degrees of movement in abstract paintings that are neither themselves moving nor depicting moving objects. These representations of movement are then systematically related to people's aesthetic evaluations, whether they are healthy controls or people with Parkinson disease.

We can also dispense with another general hypothesis. One could imagine that striatal dysfunction would impair aesthetic valuation in general. On this account, people with Parkinson disease would make aesthetic judgments that differed from healthy controls regardless of the attributes or painting under consideration. One might even predict that their judgments would be erratic in the 2AFC task for both Pollock and Mondrian paintings. This prediction was countered by the observation that healthy controls and people with Parkinson disease were similarly consistent in their comparisons of paintings. Despite this internal consistency, as we describe below, people with Parkinson disease did have altered aesthetic valuation of paintings as related to motion attributes.

Across both high-motion action paintings and lowmotion neoplastic paintings, people with Parkinson

disease gave consistently lower ratings of the amount of movement present in the art. In fact, across nine rated dimensions, motion was the only feature characterized by a main effect of group. This finding provides evidence that the brain's motor system is involved in translating nonrepresentational information from static visual cues in the image into representations of movement. There are several possible explanations for this effect. First, as proposed by the embodied simulation account of aesthetics, observers may be able to simulate the movements of artists by observing the traces of their gestural strokes in the paint (Freedberg & Gallese, 2007). Under this view, the drips and flings of paint on Jackson Pollock's canvases are represented in the brains of observers as the bodily actions required to produce those splatters. If true, our results would suggest that Parkinson disease patients are less able to translate paint traces into motor programs of the actions required to produce those patterns.

However, the fact that Mondrian's neoplastic works were also rated significantly higher in motion by controls relative to Parkinson disease patients does not cohere well with this interpretation. Mondrian's fastidious style is notable for the absence of gestural strokes in his geometric abstractions, which contrast starkly with Pollock's gestural abstractions. If there are no visible movement traces from which observers can simulate actions, to what are participants reacting when they rate the movement content of Mondrian paintings? The Mondrian paintings receiving the highest motion ratings in this study contained more visual elements, overlapping lines, repetition, and many small areas of contrasting colors. Mondrian's final Boogie-Woogie paintings, inspired by the New York jazz scene, are viewed as dynamic and rhythmic, despite an absence of gestural brushwork. The grids of yellow lines intersecting with red and blue squares are compared to New York's grid layout, the movement of traffic, blinking lights, and the stuttering rhythms of jazz. It is possible that the feeling of movement brought about by works like these results from the way these visual elements are interpreted, leading to abstract representations of movement rather than simulations of specific bodily actions. Similarly, Pollock paintings may be felt as dynamic because the increasing number of overlapping colors and the manner of paint application leads to more repetition, curvature, and contrast, which are thought to evoke feelings of movement (Peters, 2007).

The aesthetic triad model (Chatterjee & Vartanian, 2014) suggests that aesthetic experiences are emergent mental states arising from interactions between three neural systems: sensory-motor, emotion-valuation, and knowledge-meaning. Prior work suggesting that the motor system contributes to aesthetic experiences has largely been focused on motor and premotor cortical areas. The results of this paper extend these ideas by contributing to an understanding of interactions between the subcortical motor and valuation systems, both of which depend on the basal ganglia and their modulation by dopamine. However, we did not test how the knowledge-meaning component of the aesthetic triad interacts with the sensory-motor and value components in the context of Parkinson disease. It may be expected that participants who know something about Pollock and how he created his works may be more likely to simulate his actions or be biased toward interpreting the visual information in his paintings as conveying action. However, it is not clear how the link between knowledge and the motor system would be affected in Parkinson disease. Future work could test these hypotheses explicitly.

Although the data reported here cannot differentiate the exact mechanism by which motion is perceived in art, they do suggest that dysfunction of the cortico-subcortical motor circuit impairs the process of forming such movement representations. Although Parkinson disease is a heterogeneous disease, the patients studied here were early in the natural course of their disease, presenting with motor symptoms but relatively unimpaired cognition. Nevertheless, it is possible that if judging the motion content of art requires abstract, relational thinking rather than action simulation, subtle cognitive impairments not captured by standard instruments could account for the impairments seen in the Parkinson disease patients. However, the fact that motion was the only nonevaluative rating affected in Parkinson disease argues against this possibility. Judgments of other concepts like balance and complexity might also be expected to be impaired if the judgment of motion content was driven by general cognitive impairment. In addition, people with Parkinson disease demonstrated very similar levels of transitive preferences to the controls on the 2AFC task. This suggests that the patients were making sensible judgments that were internally consistent with respect to their own preferences. Moreover, on two relatively objective ratings—hue and saturation the Parkinson disease patients were again indistinguishable from controls, suggesting that their general ability to judge formal aspects of an image remains intact.

Turning to the valuation ratings of the paintings—beauty, liking, and interest—at a first pass, one might be surprised to observe that the Parkinson disease group demonstrated *increased* preferences for the Pollocks compared to the controls, whereas the controls appreciated the Mondrians more than the patients. A straightforward prediction is that people with Parkinson disease would dislike Pollock paintings and be indistinguishable from controls with Mondrian paintings. Embodied simulation accounts of aesthetics propose that simulation allows us to empathize with, understand, and connect with the artist's feelings and intentions. Why should Parkinson disease lead to an apparently enhanced appreciation of action paintings? Our analysis of the relationship between motion and preference ratings sheds some light on this issue.

Although the linear correlation strength between motion and the various appreciation ratings was low, visual inspection of the data suggested that the relationship could be quadratic. Polynomial regressions confirmed this, with models including quadratic terms for the motion-preference relationship outperforming those which included only linear terms. The interaction between group and motion ratings significantly predicted both beauty and liking ratings. Plots of the fitted regression models (Figures 3 and 4) demonstrate that the relationship between motion and aesthetic appreciation was quadratic in controls, but linear in patients. For controls, increases in motion at the low end of the scale were associated with increasing appreciation, whereas increases in motion at the high end of the scale predicted decreasing appreciation. Given that Parkinson disease patients gave significantly lower motion ratings across the board, their apparently linear relationship between motion and appreciation may reflect that their limited perception of motion falls on the ascending side of the curve. Beyond basal ganglia dysfunction, Parkinson disease is associated with abnormal functional activity in primary motor cortex (Burciu & Vaillancourt, 2018). If motor cortex is underactivated during art observation in Parkinson disease, the normal processing that leads to increased motor activity during experiences of aesthetic displeasure is likely to be disrupted, but in a systematic way. The leftward shift in forming movement representations in people with Parkinson disease would still result in internally consistent ratings as we observed in the 2AFC results.

The observed quadratic relationship between motion and aesthetic appreciation may help to clarify inconsistent findings in prior research. Whereas some studies linked increased motion to increased preference (Mastandrea & Umiltà, 2016; Ticini et al., 2014; Thakral et al., 2012), others found a negative relationship (Ishizu & Zeki, 2011; Di Dio et al., 2007; Kawabata & Zeki, 2004). We suggest the reason for this discrepancy is that the stimuli used in these studies may have been sampling different parts of the quadratic relationship we observed. As described earlier, Kawabata and Zeki (2004) suggested that the motor cortex activity previously observed in response to art may reflect preparatory

approach—avoid responses. In particular, they found that "ugly" art produced the strongest motor cortex response. The results of this study cannot speak directly to the approach—avoid hypothesis, but they do contribute more broadly to the idea that the relationship between motion perception and aesthetic value is nonlinear.

Finally, it is worth emphasizing that the motion effects found in this study cannot be attributed purely to greater complexity in the higher motion paintings. Objectively, it is true that the paintings rated highest for motion tended to also be rated as more visually complex. However, motion and complexity ratings were only correlated at .33, whereas more overlapping concepts like beauty and liking were correlated at .82. We found no significant differences in the complexity ratings given by patients and controls, whereas motion ratings were significantly lower in the patients. Furthermore, whereas the relationship between aesthetic appreciation and motion ratings was markedly different for patients and controls, the relationship between appreciation and complexity was different in strength rather than in shape. Parkinson disease patients demonstrated a steeper linear relationship between complexity and appreciation, which suggests they may find more visually intense stimuli the most appealing. Berlyne (1974) famously proposed that aesthetic preferences depend partly on the level of arousal evoked by the complexity of the stimulus. Changes in the efficacy of striatal dopamine transmission in Parkinson disease may affect the relationship between complexity and aesthetic preferences. For example, it has been suggested that pharmacological dopamine manipulation might alter the differential activation of approach-avoidance mechanisms in response to intense stimuli (Norbury & Husain, 2015). Under this view, a painting of sufficient intensity to evoke a peak aesthetic response in a control may be insufficient to elicit the same reaction in a Parkinson disease patient.

Relatedly, it should be noted that the patients in this study participated while on their usual medication. One factor not yet considered is the effect that dopaminergic medication might have on aesthetic experiences. Dopamine plays a significant role in the normal functioning of the brain's reward system, which is consequently disturbed in Parkinson disease. For example, there is an association between antiparkinsonian medications, especially dopamine agonists, and the onset of impulse control disorders (Norbury & Husain, 2015; Cools, Barker, Sahakian, & Robbins, 2003). The neurobiological effects of both dopamine dysfunction and dopaminergic medication on visual aesthetic preferences have not yet been tested experimentally and remain an important avenue for future research. A study comparing aesthetic judgments of Parkinson disease patients on and off medication would be particularly instructive.

#### Conclusion

Art appreciation is considered essential to human experience. This study provides clear evidence that altered neural functioning changes the way art is perceived and valued.

People with neurological motor dysfunction demonstrated decreased experiences of motion in art, enhanced preferences for high-motion art, and a fundamentally altered relationship between motion and aesthetic appreciation. Our results do not accord well with a straightforward embodied simulation account of aesthetics, because artworks that did not include visual traces of the artist's actions were still experienced as lower in motion by people with Parkinson disease. We suggest that visual features such as contrast, repetition, number of elements, and curvature may be apprehended metaphorically as abstract representations of movement rather than simulated as actions. Overall, we find support for hypotheses linking motion, motor responses, and aesthetic appreciation. People with Parkinson disease have altered art appreciation that is linked specifically to their altered ability to form movement representations from static abstract images.

# APPENDIX: LIST OF PAINTINGS USED AS STIMULI

Jackson Pollock paintings:

- 1. Eyes in the heat, 1946
- 2. Alchemy, 1947
- 3. Number 1A, 1948
- 4. Number 3, 1948
- 5. Untitled (Green Silver), 1949
- 6. Number 1, 1949
- 7. Autumn Rhythm (Number 30), 1950
- 8. Number 18, 1950
- 9. Convergence, 1952
- 10. The Deep, 1953

Piet Mondrian paintings:

- 1. Tableau No. 2/Composition No. VII, 1913
- Composition No.VI, Composition 9 (Blue Façade), 1914
- 3. Composition No. 10 (Pier and Ocean), 1915
- 4. Composition with Large Red Plane, Yellow, Black, Gray and Blue, 1921
- 5. Lozenge Composition with Yellow, Black, Blue, Red, and Gray, 1921
- 6. Tableau I: Lozenge with Four Lines and Gray, 1926
- 7. Composition No. II, with Red and Blue, 1929
- 8. Composition in White, Black, and Red, 1936
- 9. Composition with Yellow, Blue and Red, 1942
- 10. Victory Boogie Woogie, 1944

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Stacey Humphries: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Project administration; Visualization; Writing-Original draft; Writing-Review & editing. Jacqueline Rick: Conceptualization; Data curation; Project administration; Resources; Writing-Review & editing. Daniel Weintraub: Conceptualization; Data curation; Resources; Writing—Review & editing. Anjan Chatterjee: Conceptualization; Funding acquisition; Methodology; Project administration; Resources; Supervision; Writing—Original draft; Writing—Review & editing.

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# **Diversity in Citation Practices**

A retrospective analysis of the citations in every article published in this journal from 2010 to 2020 has revealed a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the Journal of Cognitive Neuroscience (JoCN) during this period were M(an)/M = .408, W(oman)/M = .335, M/W = .108, and W/W = .149, the comparable proportions for the articles that these authorship teams cited were M/M = .579, W/M = .243, M/W = .102, and W/W = .076(Fulvio et al., JoCN, 33:1, pp. 3–7). Consequently, JoCN encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance. The authors of this article report its proportions of citations by gender category to be as follows: M/M = .488; W/M = .488.279; M/W = .116; W/W = .116.

# **REFERENCES**

- Aharon, I., Etcoff, N., Ariely, D., Chabris, C. F., O'Connor, E., & Breiter, H. C. (2001). Beautiful faces have variable reward value: fMRI and behavioral evidence. Neuron, 32, 537–551. **DOI:** https://doi.org/10.1016/S0896-6273(01)00491-3, **PMID:**
- Ardizzi, M., Ferroni, F., Siri, F., Umiltà, M. A., Cotti, A., Calbi, M., et al. (2020). Beholders' sensorimotor engagement enhances aesthetic rating of pictorial facial expressions of pain. Psychological Research, 84, 370–379. DOI: https://doi.org/10 .1007/s00426-018-1067-7, **PMID:** 30073408
- Battaglia, F., Lisanby, S. H., & Freedberg, D. (2011). Corticomotor excitability during observation and imagination of a work of art. Frontiers in Human Neuroscience, 5, 79. **DOI:** https://doi.org/10.3389/fnhum.2011.00079, **PMID:** 21897813, **PMCID:** PMC3159953
- Belfi, A. M., Vessel, E. A., Brielmann, A., Isik, A. I., Chatterjee, A., Leder, H., et al. (2019). Dynamics of aesthetic experience are reflected in the default-mode network. Neuroimage, 188, 584–597. **DOI:** https://doi.org/10.1016/j.neuroimage.2018.12 .017, **PMID:** 30543845

- Berlyne, D. E. (1974). Studies in the new experimental aesthetics: Steps toward an objective psychology of aesthetic appreciation. Washington, DC: Hemisphere Publishing Corporation.
- Bocanegra, Y., García, A. M., Lopera, F., Pineda, D., Baena, A., Ospina, P., et al. (2017). Unspeakable motion: Selective action-verb impairments in Parkinson's disease patients without mild cognitive impairment. Brain and Language, 168, 37–46. **DOI:** https://doi.org/10.1016/j.bandl.2017.01.005, **PMID:** 28131052
- Burciu, R. G., & Vaillancourt, D. E. (2018). Imaging of motor cortex physiology in Parkinson's disease. Movement Disorders, *33*, 1688–1699. **DOI:** https://doi.org/10.1002/mds.102, **PMID:** 30280416, **PMCID:** PMC6261674
- Chatterjee, A. (2013). The aesthetic brain: How we evolved to desire beauty and enjoy art. New York: Oxford University Press. **DOI:** https://doi.org/10.1093/acprof:oso/9780199811809
- Chatterjee, A., & Vartanian, O. (2014). Neuroaesthetics. Trends in Cognitive Sciences, 18, 370–375. **DOI:** https://doi.org/10 .1016/j.tics.2014.03.003, **PMID:** 24768244
- Chatterjee, A., Widick, P., Sternschein, R., Smith, W. B., & Bromberger, B. (2010). The assessment of art attributes. Empirical Studies of the Arts, 28, 207-222. DOI: https://doi .org/10.2190/EM.28.2.f
- Concerto, C., Infortuna, C., Mineo, L., Pereira, M., Freedberg, D., Chusid, E., et al. (2016). Observation of implied motion in a work of art modulates cortical connectivity and plasticity. Journal of Exercise Rehabilitation, 12, 417–423. DOI: https://doi.org/10.12965/jer.1632656.328, **PMID:** 27807519, **PMCID:** PMC5091056
- Cools, R., Barker, R. A., Sahakian, B. J., & Robbins, T. W. (2003). L-Dopa medication remediates cognitive inflexibility, but increases impulsivity in patients with Parkinson's disease. Neuropsychologia, 41, 1431–1441. DOI: https://doi.org/10 .1016/S0028-3932(03)00117-9, **PMID:** 12849761
- Di Dio, C., Macaluso, E., & Rizzolatti, G. (2007). The golden beauty: Brain response to classical and renaissance sculptures. PLoS One, 2, e1201. DOI: https://doi.org/10.1371/journal .pone.0001201, **PMID:** 18030335, **PMCID:** PMC2065898
- Faust, N. T., Chatterjee, A., & Christopoulos, G. I. (2019). Beauty in the eyes and the hand of the beholder: Eye and hand movements' differential responses to facial attractiveness. Journal of Experimental Social Psychology, 85, 103884. DOI: https://doi.org/10.1016/j.jesp.2019.103884
- Fernandino, L., Conant, L. L., Binder, J. R., Blindauer, K., Hiner, B., Spangler, K., et al. (2013). Parkinson's disease disrupts both automatic and controlled processing of action verbs. Brain and Language, 127, 65–74. **DOI:** https://doi.org/10.1016/j .bandl.2012.07.008, **PMID:** 22910144, **PMCID:** PMC3574625
- Freedberg, D., & Gallese, V. (2007). Motion, emotion and empathy in esthetic experience. Trends in Cognitive Sciences, 11, 197–203. **DOI:** https://doi.org/10.1016/j.tics .2007.02.003, **PMID:** 17347026
- Galvan, A., & Wichmann, T. (2008). Pathophysiology of Parkinsonism. Clinical Neurophysiology, 119, 1459–1474. **DOI:** https://doi.org/10.1016/j.clinph.2008.03.017, **PMID:** 18467168, **PMCID:** PMC2467461
- Helmich, R. C., de Lange, F. P., Bloem, B. R., & Toni, I. (2007). Cerebral compensation during motor imagery in Parkinson's disease. Neuropsychologia, 45, 2201–2215. DOI: https://doi .org/10.1016/j.neuropsychologia.2007.02.024, **PMID:** 17448507
- Humphries, S., Holler, J., Crawford, T. J., Herrera, E., & Poliakoff, E. (2016). A third-person perspective on co-speech action gestures in Parkinson's disease. Cortex, 78, 44-54. **DOI:** https://doi.org/10.1016/j.cortex.2016.02.009, **PMID:** 26995225, PMCID: PMC4865523
- Humphries, S., Klooster, N., Cardillo, E., Weintraub, D., Rick, J., & Chatterjee, A. (2019). From action to abstraction: The

- sensorimotor grounding of metaphor in Parkinson's disease. *Cortex*, *121*, 362–384. **DOI:** https://doi.org/10.1016/j.cortex .2019.09.005, **PMID:** 31678683, **PMCID:** PMC6903422
- Ishizu, T., & Zeki, S. (2011). Toward a brain-based theory of beauty. PLoS One, 6, e21852. DOI: https://doi.org/10.1371/journal .pone.0021852, PMID: 21755004, PMCID: PMC3130765
- Kable, J. W., Kan, I. P., Wilson, A., Thompson-Schill, S. L., & Chatterjee, A. (2005). Conceptual representations of action in the lateral temporal cortex. *Journal of Cognitive Neuroscience*, 17, 1855–1870. DOI: https://doi.org/10.1162/089892905775008625, PMID: 16356324
- Kable, J. W., Lease-Spellmeyer, J., & Chatterjee, A. (2002). Neural substrates of action event knowledge. *Journal of Cognitive Neuroscience*, 14, 795–805. **DOI:** https://doi.org/10.1162/08989290260138681, **PMID:** 12167263
- Kawabata, H., & Zeki, S. (2004). Neural correlates of beauty. Journal of Neurophysiology, 91, 1699–1705. DOI: https://doi.org/10.1152/jn.00696.2003, PMID: 15010496
- Kim, C.-Y., & Blake, R. (2007). Brain activity accompanying perception of implied motion in abstract paintings. *Spatial Vision*, 20, 545–560. **DOI:** https://doi.org/10.1163/156856807782758395, **PMID:** 18338460
- Knoblich, G., Seigerschmidt, E., Flach, R., & Prinz, W. (2002). Authorship effects in the prediction of handwriting strokes: Evidence for action simulation during action perception. Quarterly Journal of Experimental Psychology, 55, 1027–1046. DOI: https://doi.org/10.1080/02724980143000631, PMID: 12188508
- Kourtzi, Z., & Kanwisher, N. (2000). Activation in human MT/MST by static images with implied motion. *Journal of Cognitive Neuroscience*, 12, 48–55. **DOI:** https://doi.org/10.1162/08989290051137594, **PMID:** 10769305
- Lauring, J. O., Pelowski, M., Specker, E., Ishizu, T., Haugbøl, S., Hollunder, B., et al. (2019). Parkinson's disease and changes in the appreciation of art: A comparison of aesthetic and formal evaluations of paintings between PD patients and healthy controls. *Brain and Cognition*, 136, 103597. **DOI:** https://doi.org/10.1016/j.bandc.2019.103597, **PMID:** 31491732
- Leder, H., Bär, S., & Topolinski, S. (2012). Covert painting simulations influence aesthetic appreciation of artworks. *Psychology Science*, 23, 1479–1481. **DOI:** https://doi.org/10.1177/0956797612452866, **PMID:** 23137968
- Lindenbach, D., & Bishop, C. (2013). Critical involvement of the motor cortex in the pathophysiology and treatment of Parkinson's disease. *Neuroscience and Biobehavioral Reviews*, 37, 2737–2750. DOI: https://doi.org/10.1016/j.neubiorev.2013 .09.008, PMID: 24113323, PMCID: PMC3859864
- Longcamp, M., Anton, J.-L., Roth, M., & Velay, J.-L. (2005). Premotor activations in response to visually presented single letters depend on the hand used to write: A study on left-handers. *Neuropsychologia*, 43, 1801–1809. **DOI:** https://doi.org/10.1016/j.neuropsychologia.2005.01.020, **PMID:** 16154456
- Longcamp, M., Tanskanen, T., & Hari, R. (2006). The imprint of action: Motor cortex involvement in visual perception of handwritten letters. *Neuroimage*, *33*, 681–688. **DOI:** https://doi.org/10.1016/j.neuroimage.2006.06.042, **PMID:** 16965922
- Mastandrea, S., & Umiltà, M. A. (2016). Futurist art: Motion and aesthetics as a function of title. *Frontiers in Human Neuroscience*, *10*, 201. **DOI:** https://doi.org/10.3389/fnhum.2016.00201, **PMID:** 27242471, **PMCID:** PMC4868917
- Menninghaus, W., Wagner, V., Wassiliwizky, E., Schindler, I., Hanich, J., Jacobsen, T., et al. (2019). What are aesthetic emotions? *Psychological Review*, *126*, 171–195. **DOI:** https://doi.org/10.1037/rev0000135, **PMID:** 30802122
- Nakamura, K., & Kawabata, H. (2015). Transcranial direct current stimulation over the medial prefrontal cortex and left primary motor cortex (mPFC-lPMC) affects subjective beauty

- but not ugliness. *Frontiers in Human Neuroscience*, *9*, 654. **DOI:** https://doi.org/10.3389/fnhum.2015.00654, **PMID:** 26696865, **PMCID:** PMC4672048
- Nasreddine, Z. S., Phillips, N. A., Bédirian, V., Charbonneau, S., Whitehead, V., Collin, I., et al. (2005). The Montreal Cognitive Assessment, MoCA: A brief screening tool for mild cognitive impairment. *Journal of the American Geriatrics Society*, 53, 695–699. DOI: https://doi.org/10.1111/j.1532-5415.2005 .53221.x, PMID: 15817019
- Norbury, A., & Husain, M. (2015). Sensation-seeking: Dopaminergic modulation and risk for psychopathology. *Behavioral Brain Research*, *288*, 79–93. **DOI:** https://doi.org/10.1016/j.bbr.2015.04.015, **PMID:** 25907745
- Osaka, N., Matsuyoshi, D., Ikeda, T., & Osaka, M. (2010). Implied motion because of instability in Hokusai Manga activates the human motion-sensitive extrastriate visual cortex: An fMRI study of the impact of visual art. *NeuroReport*, *21*, 264–267. **DOI:** https://doi.org/10.1097/WNR.0b013e328335b371, **PMID:** 20125056
- Peters, G. (2007). Aesthetic primitives of images for visualization. In *Proceedings of the 11th International Conference on Information Visualization* (pp. 316–325). Zurich, Switzerland: IEEE. **DOI:** https://doi.org/10.1109/IV.2007.20
- Poliakoff, E. (2013). Representation of action in Parkinson's disease: Imagining, observing, and naming actions. *Journal of Neuropsychology*, 7, 241–254. **DOI:** https://doi.org/10.1111/jnp.12005, **PMID:** 23320735
- Proverbio, A. M., Riva, F., & Zani, A. (2009). Observation of static pictures of dynamic actions enhances the activity of movement-related brain areas. *PLoS One*, 4, e5389. **DOI:** https://doi.org/10.1371/journal.pone.0005389, **PMID:** 19421311, **PMCID:** PMC2671843
- Sbriscia-Fioretti, B., Berchio, C., Freedberg, D., Gallese, V., & Umiltà, M. A. (2013). ERP modulation during observation of abstract paintings by Franz Kline. *PLoS One*, 8, e75241. DOI: https://doi.org/10.1371/journal.pone.0075241, PMID: 24130693, PMCID: PMC3793982
- Senior, C., Barnes, J., Giampietro, V., Simmons, A., Bullmore, E. T., Brammer, M., et al. (2000). The functional neuroanatomy of implicit-motion perception or representational momentum. *Current Biology*, 10, 16–22. **DOI:** https://doi.org/10.1016/S0960 -9822(99)00259-6, **PMID:** 10660297
- Taylor, J. E. T., Witt, J. K., & Grimaldi, P. J. (2012). Uncovering the connection between artist and audience: Viewing painted brushstrokes evokes corresponding action representations in the observer. *Cognition*, 125, 26–36. **DOI:** https://doi.org/10 .1016/j.cognition.2012.06.012, **PMID:** 22986017
- Thakral, P. P., Moo, L. R., & Slotnick, S. D. (2012). A neural mechanism for aesthetic experience. *NeuroReport*, *23*, 310–313. **DOI:** https://doi.org/10.1097/WNR.0b013e328351759f, **PMID:** 22357395
- Ticini, L. F., Rachman, L., Pelletier, J., & Dubal, S. (2014). Enhancing aesthetic appreciation by priming canvases with actions that match the artist's painting style. *Frontiers in Human Neuroscience*, 8, 391. **DOI:** https://doi.org/10.3389/fnhum.2014.00391, **PMID:** 24917808, **PMCID:** PMC4043134
- Umiltà, M. A., Berchio, C., Sestito, M., Freedberg, D., & Gallese, V. (2012). Abstract art and cortical motor activation: An EEG study. Frontiers in Human Neuroscience, 6, 311. DOI: https://doi.org/10.3389/fnhum.2012.00311, PMID: 23162456, PMCID: PMC3499799
- 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. **DOI:** https://doi.org/10.1523/JNEUROSCI.1289-06.2006, **PMID:** 16870739, **PMCID:** PMC6674209
- van Nuenen, B. F. L., Helmich, R. C., Buenen, N., van de Warrenburg, B. P. C., Bloem, B. R., & Toni, I. (2012).

- Compensatory activity in the extrastriate body area of Parkinson's disease patients. *Journal of Neuroscience*, *32*, 9546–9553. **DOI:** https://doi.org/10.1523/JNEUROSCI.0335-12.2012, **PMID:** 22787040, **PMCID:** PMC6622256
- Vessel, E. A., Isik, A. I., Belfi, A. M., Stahl, J. L., & Starr, G. G. (2019). The default-mode network represents aesthetic appeal that generalizes across visual domains. *Proceedings of the National Academy of Sciences, U.S.A.*, 116, 19155–19164. **DOI:** https://doi.org/10.1073/pnas.1902650116, **PMID:** 31484756, **PMCID:** PMC6754616
- Vessel, E. A., Starr, G. G., & Rubin, N. (2012). The brain on art: Intense aesthetic experience activates the default mode network. *Frontiers in Human Neuroscience*, *6*, 66. **DOI:** https://doi.org/10.3389/fnhum.2012.00066, **PMID:** 22529785, **PMCID:** PMC3330757
- Vessel, E. A., Starr, G. G., & Rubin, N. (2013). Art reaches within: Aesthetic experience, the self and the default mode network. *Frontiers in Neuroscience*, 7, 258. **DOI:** https://doi.org/10.3389/fnins.2013.00258, **PMID:** 24415994, **PMCID:** PMC3874727

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